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Redescription and Life History of *Tytodectes strigis* (Acari: Hypoderatidae), a Parasite of the Barn Owl *Tyto alba* (Aves: Strigidae)

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With 67 figures and 3 tables

Summary

All developmental stages of *Tytodectes strigis* (Gené, 1845) are described and figured, using light and electron microscopical techniques. The previous descriptions of the genus *Tytodectes* are corrected for the deutonymph in two points: genu I and II bear one solenidion each and the total number of setae on tarsus I is nine, one of the setae (aa) has obviously been transformed into a strain detector. In respect of the problem of the host species we arrive at the conclusion that the first description unequivocally refers to the barn owl *Tyto alba*. As a special feature of its life cycle, *T. strigis* has retained facultative hypopody. This is interpreted as adaptation to the reproduction biology of the host which can produce two clutches in one year. Data on the abundance of *T. strigis* both in the nests and inside the owls are given and the locations of the deutonymphs in the owls are described and illustrated.

Zusammenfassung

Sämtliche Entwicklungsstadien von *Tytodectes strigis* (Gené, 1845) werden beschrieben und unter Verwendung licht- und elektronenmikroskopischer Techniken abgebildet. Die bisherigen Beschreibungen der Gattung *Tytodectes* werden für die Deutonymphe in zwei Punkten korrigiert: Genu I and II tragen je eine Solenidie und die Gesamtzahl der Setae an Tarsus I beträgt neun, von denen eine Borste (aa) offensichtlich in einen Dehnungs-Detektor umgewandelt wurde. Im Hinblick auf die Wirtstier-Problematik kommen wir zu dem Ergebnis, daß sich die Erstbeschreibung hierin eindeutig auf die Schleiereule *Tyto alba* bezieht. Der Entwicklungszyklus von *T. strigis* weist als Besonderheit die Beibehaltung der fakultativen Hypopodie auf, was als Anpassung an die Brutbiologie des Wirtes (Vorkommen von Zweitbruten) gedeutet wird. Zahlen zur Häufigkeit von *T. strigis* in den Horsten wie auch in den Eulen werden gegeben und die Aufenthaltsorte der Deutonymphen in den Eulen beschrieben und abgebildet.

Contents

1. Introduction

The Hypoderatidae are temporarily parasitic nidicolous associates of vertebrates. The great majority of them (Hypoderatinae) depends on birds. A few species (Muridectinae) have been found on rodents, but so far they are known only as deutonymph (hypopus). Because of their unusual mode of development, the Hypoderatinae hold an extraordinary position among the astigmatic mites: while the deutonymphs in all other Astigmata are non-feeding instars adapted for dispersal or survival under adverse conditions, in the Hypoderatinae they penetrate the skin of their host birds and accumulate in the connective tissues. Here, the deutonymphs feed in a way still unknown thereby increasing considerably. In the course of the parasitic period, the cuticle is altered and microstructurally modified. During the breeding period, the enlarged and mature hypopi leave their host birds and develop into adults.

Since the non-parasitic stages live exclusively in the nests of their hosts, which in most cases are hardly accessible, up to the 1960s, the Hypoderatinae were only known as hypopi and were erraneously regarded as the deutonymphs of feather mites.

The redescription and documentation of the life cycle of *Tytodectes strigis* presented in this study resulted from field work initiated by the Vogelschutzwarte Karlsruhe aiming at the evaluation of the influence of nidicolous parasites on the breeding success of some selected indigenous birds.

2. Materials, Methods and Acknowledgements

2.1. Materials

In the years 1992 (areas of Karlsruhe and Heilbronn, SW-Germany), 1994 (area of Vaihingen/Enz, SW-Germany), 1995 (areas of Vaihingen/Enz and Heilbronn) and 1996 (area of Vaihingen/Enz) samples (approximately 500 ml per sample) of nest material from nestboxes of *T. alba* were collected during controlling or ringing of nestlings. For detailed description of location of nests and estimated age of the oldest nestling at the date of sampling see table 1.

For observations on the parasitic deutonymphs, dead (mostly road killed) specimens of the barn owl were used. For data of locations and sources see table 2.

2.2. Methods

Samples of nest material were observed under a stereo microscope (magnifications 16x and 40x). In the same manner the barn owls were inspected for mites. For this, the owls were skinned and the subcutaneous connective tissue was then carefully inspected, paying particular attention to the legs.

The mites were reared in the laboratory in their natural substrate. For this, infested nest material was placed in plastic bags and regularly sprayed with water in order to maintain adequate humidity.

For light microscopy, the mites were mounted in Hoyer's fluid. Drawings were made with the aid of a Zeiss drawing apparatus.

Light micrographs were made by using the photomicroscopes Standard Universal and Axiophot (Zeiss) and a stereomicroscope (Wild M 400).

For SEM-investigations, the mites were killed by freezing and were subsequently washed with a tenside. Further preparation was performed according to the procedure by Bock (1987): fixation by a modified Carnoy (acetic acid : chloroforme : abs. ethanol = 1 : 1 : 3) (at least 4 hrs), abs. ethanol (5–10 min), hexamethyldisilazane (5 min), air-drying. Sputtering with gold. SEM DSM 940 (Zeiss).

The nomenclature of idiosomal chaetotaxy follows Griffiths et alii (1990). In so doing, we simply want to favour the establishment of a standardization. It does not mean, however, that we follow the fundamental idea behind the argumentation developed by these authors that segments are added during the ontogenetic development of acariform mites, irrespective of the possible correctness of its conclusions. Nomenclature of leg chaetotaxy follows Griffiths (1964) and Fain (1967b).

2.3. Acknowledgements

Tyto alba is a protected bird species in Germany. This, and because of the hardly accessible habitat of the free living instars, the search for *T. strigis* could only be successful by the extensive assistence of a large number of persons. For their generous help we thank the following persons: samples of nest material were collected by Dr. R. Altmüller (Lachendorf), H. Furrington (Heilbronn), U. Hoffmann (Karlsruhe), H. Keil (Oberriexingen) and the members of the "AG zum Schutz bedrohter Eulen". Dead barn owls were provided by E. Gabler (Sindelfingen), H. Keil, Dr. C. Köppel (Gaggenau), Dr. D. Mörike (Stuttgart), Dr. T. Pfister (Lausen) and E. Wendt (Asperg). B. Curth (Stuttgart) assisted in the SEM techniques and W. Lang (Waiblingen) and B. Schmid (Stuttgart) in the realization of some of the drawings. S. Hederer (Germering) translated several important passages from Russian texts and Dr. M. Sosoro (Augsburg) translated the papers of Gené and De Filippi. Dr. A. Palermo (Heidelberg) provided the explanation of a vernacular name of the barn owl. Prof. Dr. B. Frank and W. Jansen (Stuttgart) critically read the manuscript and gave valuable comments.

3. Historical Record

The earliest account on the presence of subcutaneous mites in owls which can clearly be referred to *T. strigis* is by F. C. H. Creplin (1844). In a footnote, he reports on two "*Strix flammea*" in which a large amount of mites was assembled "like fish roe" under the skin of the heel joints of both legs. Creplin gives a short description of the mites but does not provide a species name. He notes that he has given the mites to the Zoological Museum in Greifswald.

On September 23th 1845 G. Gené, professor in Torino, reported to the members of the "Sezione di zoologia della sesta riunione degli Scienziati Italiani" on a "sarc-

Table 1. Presence (+) or absence (–) of *Tytodectes strigis* in the nest material of 33 *Tyto alba* nests inspected between June 1992 and August 1996. The estimated age of the oldest nestling at the date of sampling and the number of nestlings at the date of sampling is given. – Abbreviation: *d* = days.

Date of sampling	Location of sampling; names of nestboxes in backets *( )*	Presence of *(Tytodectes strigis*	Estimated age of the oldest nestling (±7 d)	Number of nestlings
22. 06. 92	Ettlingen-Oberweier	+	25 d	4
29. 06. 92	Palmbach (Kir.)	+	20 d	5
09. 07. 92	Heilbronn-Böckingen	+	35 d	5
03. 08. 94	Enzweihingen (Kinz.)	–	35 d	4
04. 08. 94	Gündelbach (Schi.)	–	40 d	5
06. 08. 94	Vaihingen/Enz (Nonn.)	+	65 d	4
06. 08. 94	Vaihingen/Enz (Bless.)	–	55 d	2
22. 06. 95	Hausen a. d. Zaber (Kir.)	–	21 d	3
22. 06. 95	Hausen a. d. Zaber	–	28 d	4
23. 06. 95	Binswangen	–	28 d	4
28. 06. 95	Abstetterhof	–	28 d	4
28. 06. 95	Unterheinriet	–	21 d	4
28. 06. 95	Jettenbach	–	21 d	4
28. 06. 95	Wüstenhausen	–	28 d	3
28. 06. 95	Neckarwestheim	–	28 d	5
28. 06. 95	Talheim	–	35 d	5
30. 06. 95	Bonfeld (I)	–	35 d	7
30. 06. 95	Bonfeld (II)	–	28 d	7
30. 06. 95	Untereisesheim	–	28 d	5
05. 07. 95	Ilsfeld-Landturm	–	28 d	2
21. 07. 95	Weinsberg	–	21 d	3
19. 06. 95	Kleinglattbach (Bl.)	–	28 d	6
19. 06. 95	Aurich (Zahn)	–	20 d	3
06. 07. 95	Horrheim (Stie.)	–	26 d	5
06. 07. 95	Horrheim (Lad.)	–	28 d	3
07. 07. 95	Sersheim (Grau)	–	28 d	4
09. 07. 95	Vaihingen/Enz (Nonn.)	–	32 d	5
18. 07. 95	Ochsenbach (Scho.)	–	49 d	5
15. 06. 96	Vaihingen/Enz (Nonn.)	–	26 d	3
23. 08. 96	Gündelbach (Schi.)	–	93 d*	6
23. 08. 96	Gündelbach (Men.)	–	103 d*	6
23. 08. 96	Vaihingen/Enz (Bless.)	+	100 d*	6
23. 08. 96	Sachsenheim-Rechentshofen	–	96 d*	7

* nestlings had fledged weeks ago

optid" mite he had found in all "*Strix flammea*" in the vicinity of Torino. Additional names GENÉ used for the host were the term "barbagianni" and the vernacular name "dama". As provisional name for the mites he proposed "*Sarcoptes strigis*". He also mentioned his fruitless efforts to find the mite in *Otus scops, Strix aluco* ("assiuoli, allocchi") and "other nocturnal birds more closely related to *Strix flammea*" (". . . sugli altri uccelli notturni che più sono affini alla *Strix flammea* . . .").

Table 2. Presence (+) or absence (–) of *Tytodectes strigis* in 19 *Tyto alba* specimens. – For explication of the locations (sites A, B, C, D) of the mites inside the birds see chapter 4.6. and figs. 50 and 51.

Owl no.	Sex	Location (city/town)	Date of collection	Date and location of ringing; name of nestbox in brackets ( ).	Source of owl material	Presence of *Tytodectes strigis* (total number in both legs)	Location inside the bird
1	?	Gaggenau	20. 01. 94	21. 06. 93 Ettlingen-Oberweier	C. Köppel	+	A, B
2	f	Braunsbach near Schw. Hall	09. 01. 95	–	E. Wendt	–	–
3	?	Tamm near Ludwigsburg	08. 03. 95	–	E. Wendt	+	A
4	?	region of Freiburg i. B.	before 25. 03. 96	–	Naturkundemus. Stuttgart	–	–
5	m	region of Feriburg i. B.	before 25. 03. 96	–	Naturkundemus. Stuttgart	+	A, C
6	f	region of Sindelfingen	before 26. 03. 96	–	E. Gabler	+	A
7	f	region of Sindelfingen	before 26. 03. 96	–	E. Gabler	–	–
8	m	region of Sindelfingen	before 26. 03. 96	–	E. Gabler	+	A
9	m	Schwäbisch Hall	17. 11. 95	20. 07. 95 Rosengarten-Wilhelmsglück	E. Wendt	–	–
10	f	?	before Dec. 95	–	E. Wendt	+ (3)	A
11	f	Schwäbisch Hall	11. 03. 96	05. 06. 93 Criesbach	E. Wendt	–	–
12	f	region of Schwäb. Hall	before April 96	–	E. Wendt	+	A, B, D
13	m	region of Vaihingen/Enz	winter 95/96	–	H. Keil	+	A, B, D
14	f	region of Vaihingen/Enz	winter 95/96	–	H. Keil	–	–
15	m	region of Vaihingen/Enz	winter 95/96	19. 06. 95 Eberdingen-Hochdorf	H. Keil	+	A, B, C, D
16	m	region of Vaihingen/Enz	winter 95/96	–	H. Keil	+ (1)	A
17	f	region of Vaihingen/Enz	winter 95/96	16. 10. 93 Sersheim	H. Keil	+	A
18	m	Pligny/Dombes (F)	02. 06. 96	–	E. Wendt	–	–
19	f	Gündelbach	07. 07. 96	27. 06. 96 Gündelbach (Men.)	H. Keil	+ (5)	A

Obviously he did not know about Creplin's publication from the preceding year, for he did not cite it in his discussion of the finding. A part of Gené's report appeared in the proceedings (Atti della Riunione degli Scienziati Italiani 1845: 409–410). The complete text of his contribution was published posthumously (Gené 1848) together with drawings of the ventral and dorsal face of *S. strigis*.

Filippo De Filippi (1861) describes more Hypoderatids from diverse birds and introduces the generic name "*Hypodectes*" for this peculiar group of mites. Based on own investigations, he confirms Gené, who had stated that obviously all "*Strix flammea*" or "barbagianni" of Piedmont were infested by "*Hypodectes strigis*". De Filippi is also the first who draws the correct conclusion from his observations (lack of sexual organs, equality of developmental level, four pairs of legs) that the *Hypodectes*-mites found in the birds are in fact postlarval juvenile instars. Because of the lack of a "distinct mouth (bocca distinta)" he relates these instars with the hypopi. He presumes that the remaining developmental stages (adults, eggs and larva; the proto- and tritonymph were not yet discriminated within the "nymphal stage") could be found in the nests of the respective birds.

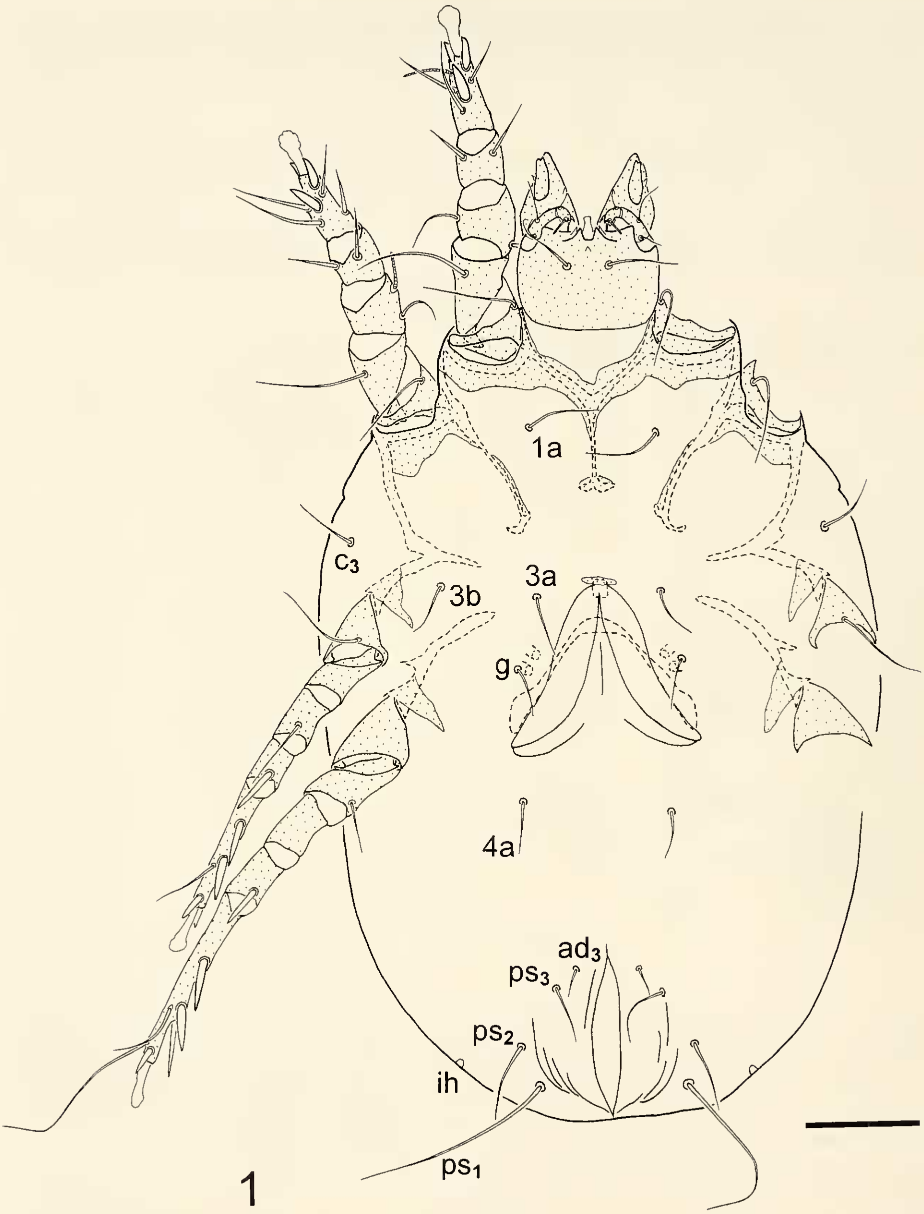
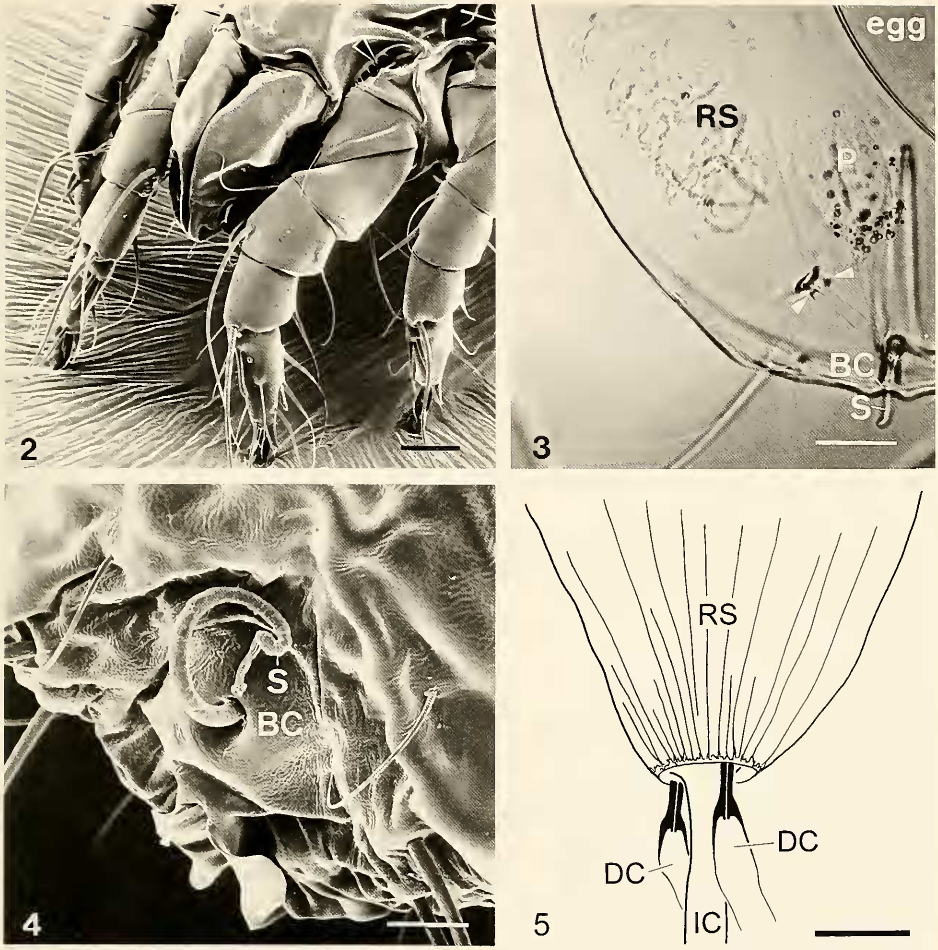


Fig. 1. *Tytodectes strigis*, female; ventral view, left legs partly omitted. – Scale bar: 50 µm.

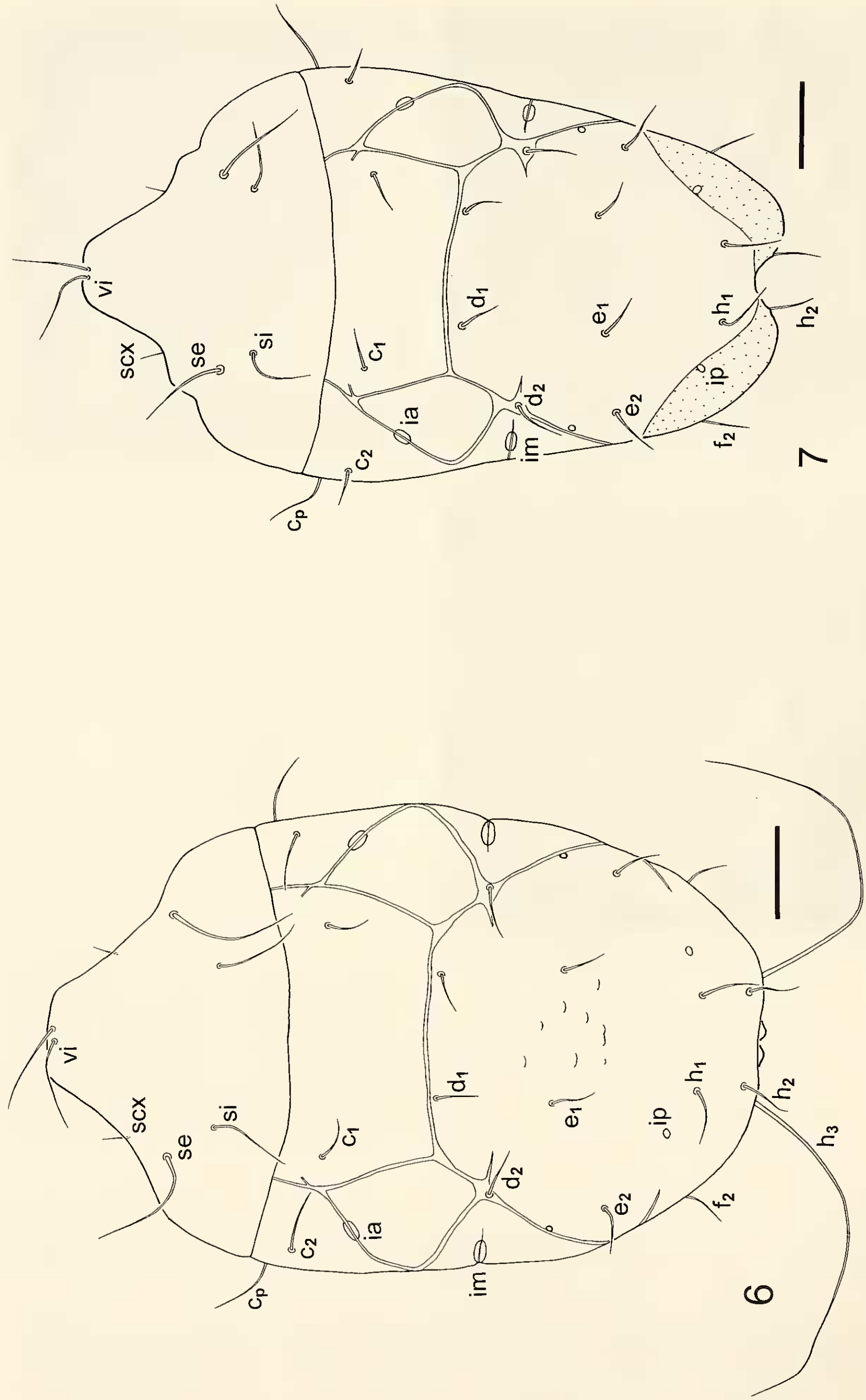
Such a systematic investigation of birds nests, however, was not done. On the contrary: the research on Hypoderatids suffered a setback when ROBIN & MÉGNIN (1877: 238) declare them to be the deutonymphs of feather mites. This view is again emphasized by MÉGNIN (1879) in an extensive review on the endoparasitic mites of birds. Since both authors belonged to the leading acarologists of their time, their notion was generally accepted and persisted up to the 1960s.



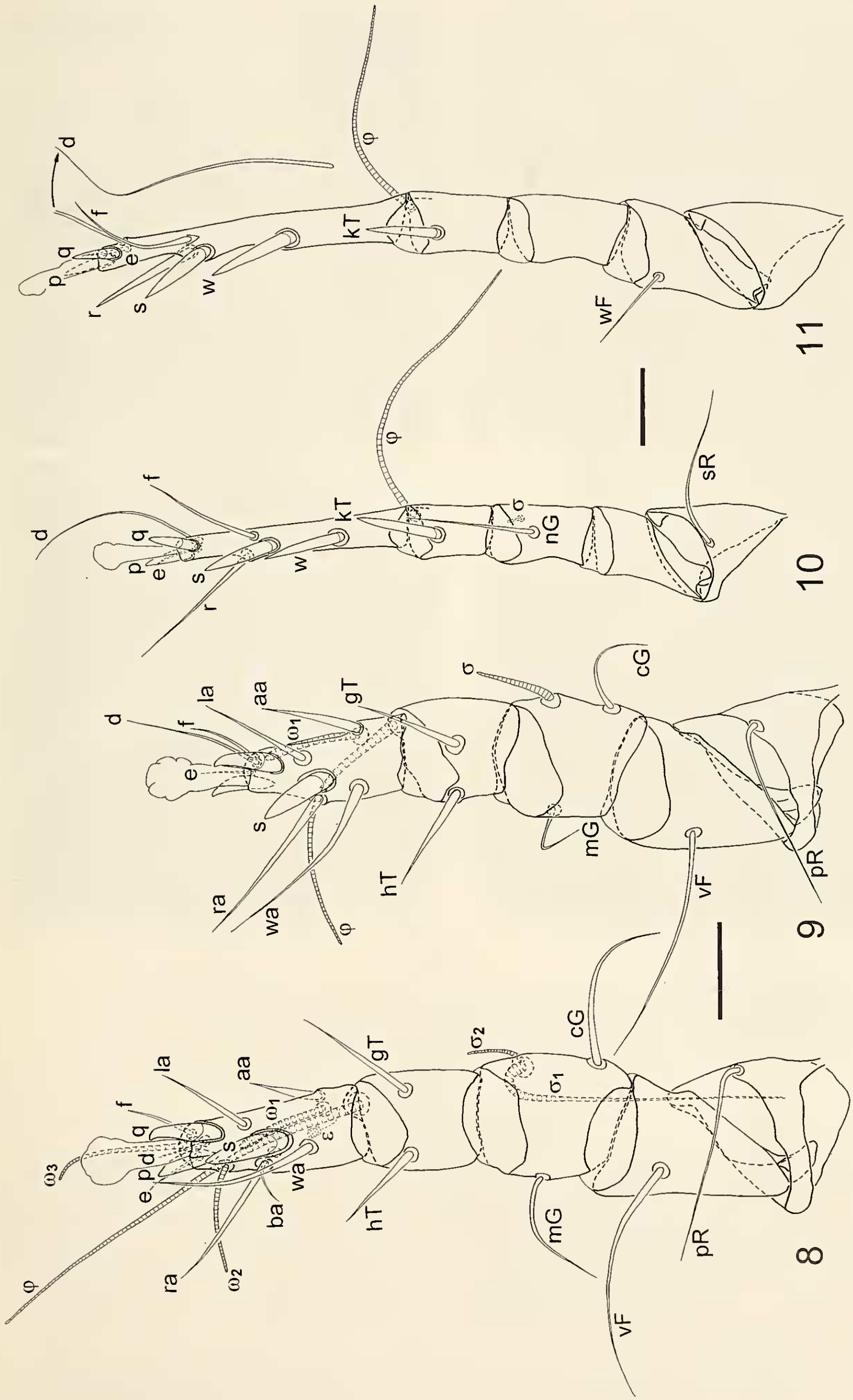
Figs. 2–5. *Tytodectes strigis*, female. – 2. Frontal view; *arrowhead* = opening of supracoxal gland (scale bar: 20 µm); – 3. opisthosoma (light micrograph); *BC* = bursa copulatrix, *P* = fecal pellet, *RS* = sac of receptaculum seminis containing putative spermatophores; *S* = putative spermatophore; *arrowheads*: proximal parts of ductus conjunctivi that lead to the ovaries (scale bar: 25 µm); – 4. bursa copulatrix (*BC*) with putative spermatophore (*S*) (scale bar: 10 µm); – 5. basal parts of receptaculum seminis; *DC* = ductus conjunctivus, *IC* = inseminatory canal, *RS* = sac of receptaculum seminis (scale bar: 10 µm).

VITZTHUM (1934) in his description of *Neottialges vitzthumi* (as the "deutonymph of *Pterolichus nisi*") cites the entire literature on the valid or possible subcutaneous deutonymphs, regarding the barn owl *Tyto alba* as the host of "*Sarcoptes strigis*".

Subsequently, however, some confusion arose as to the question to which species belongs the host of *T. strigis* since "*Strix flammea*" could be referred to two different species: *Strix flammea* Linné = *Tyto alba* (Scopoli) (barn owl) or *Strix flammea* Pontoppidan = *Asio flammeus* (Pontopp.) (short-eared owl) (HARTERT 1912–21; PETERS 1940). Consequently OUDEMANS (1937) identifies in his "Kritisch Historisch Overzicht Der Acarologie", Vol. E "barbagianni" with *Otus otus* (= *Asio otus*) and *Otus*



Figs. 6–7. *Tytodectes strigis*. – 6. Female; idiosoma, dorsal view (scale bar: 50 µm); – 7. male; idiosoma, dorsal view (scale bar: 40 µm).



Figs. 8–11. *Tytodectes strigis*, female. – 8. Leg I; – 9. leg II (scale bar figs. 8–9: 20 µm); – 10. leg III; – 11. leg IV (scale bar figs. 10–11: 20 µm).

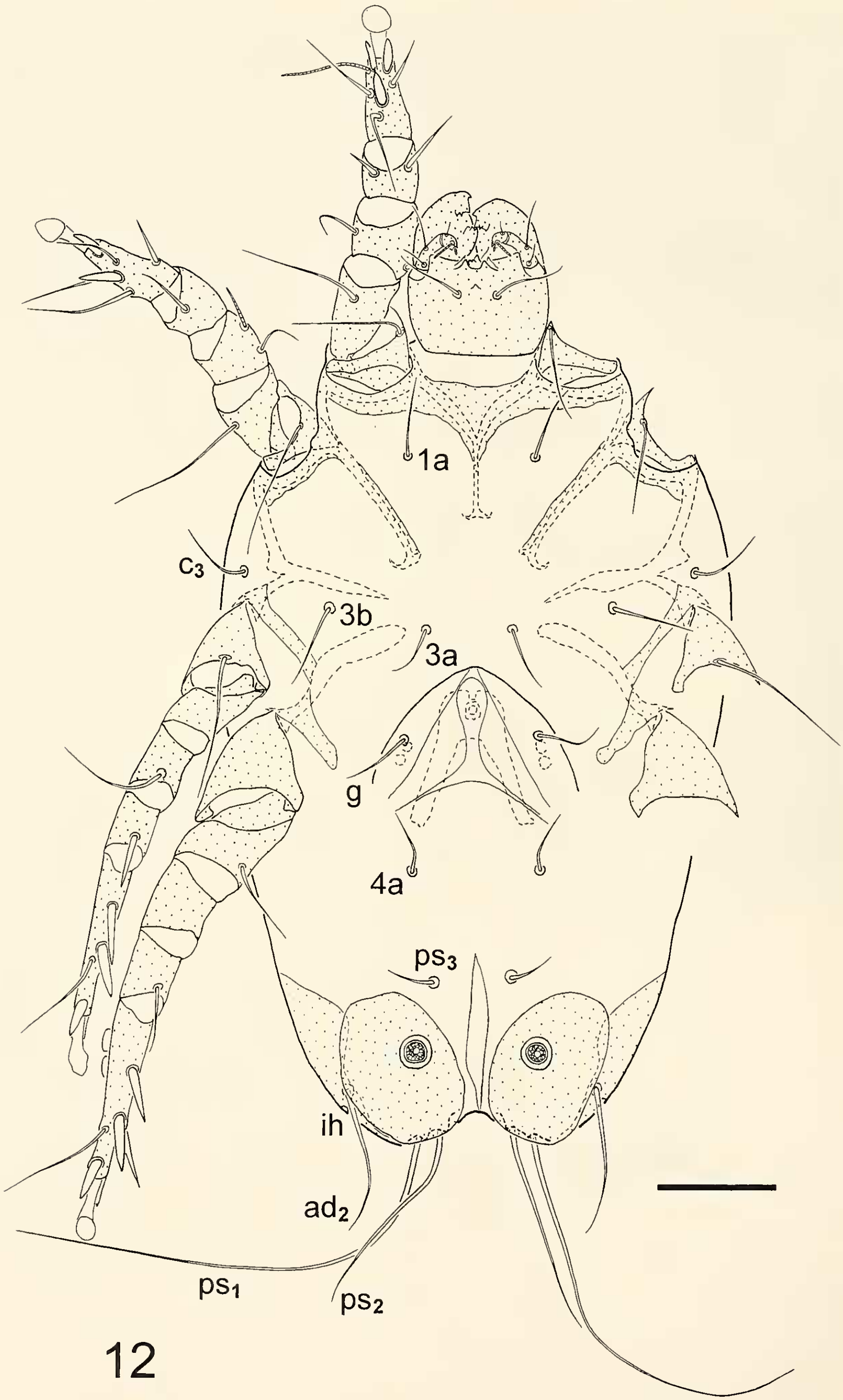
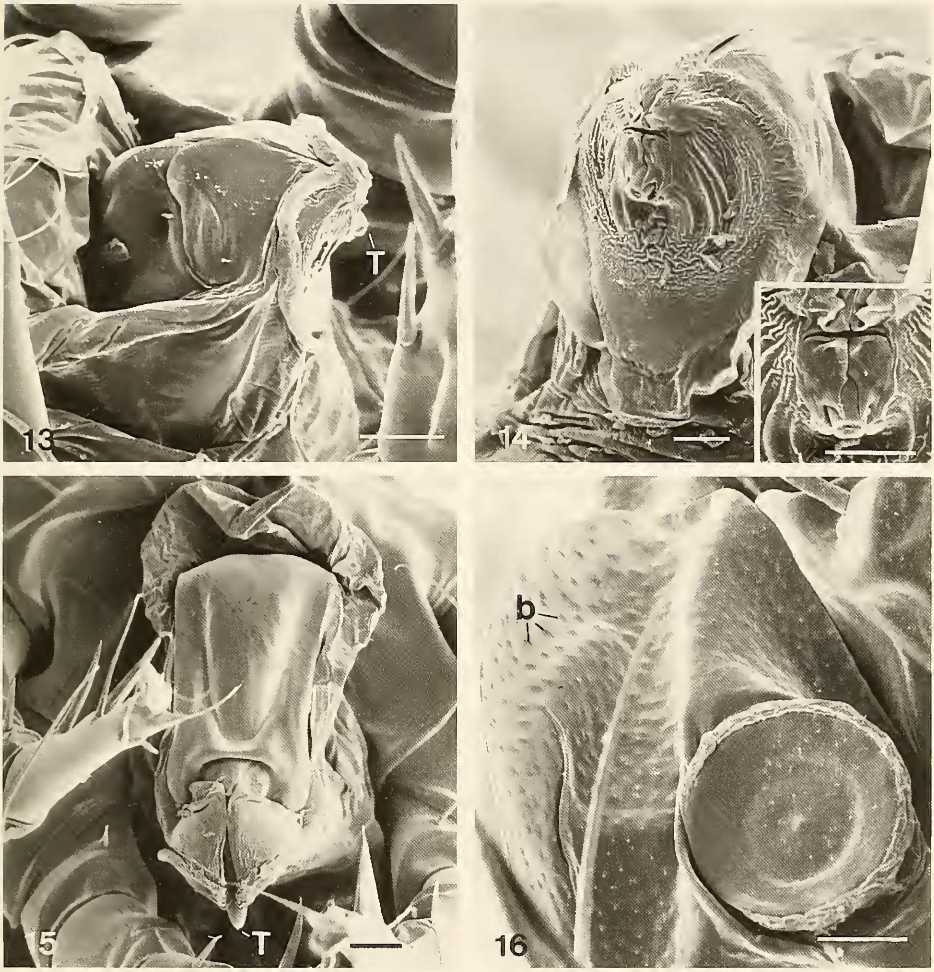


Fig. 12. *Tytodectes strigis*, male; ventral view, left legs partly omitted. – Scale bar: 45 µm.



Figs. 13–16. *Tytodectes strigis*, male. – 13. Aedeagus, lateral view; *T* = tip of aedeagus (scale bar: 10 µm); – 14. aedeagus, frontal view (*inset*: tip of aedeagus, frontal view) (scale bars: 5 µm); – 15. aedeagus, extremely protruded (probably unphysiologically); *T* = tip of aedeagus (scale bar: 10 µm); – 16. left adanal copulatory sucker with surrounding rim; *b* = bump (scale bar: 5 µm).

accipitrinus (= *Asio flammeus*) (not *Otus otus* or *Otus accipitrinus* as quoted by Fain 1967a). Oudemans, however, succeeded in receiving Creplin's material from the Zoological Institute in Greifswald which gave rise to several drawings (ventral, dorsal and lateral view and details of legs I–IV). They are reproduced in the "Overzicht" combined with a short description. According to prevailing opinions, Oudemans allocates these deutonymphs to the feather mite *Kramerella lunulata*.

Under the headings "*Gabucinia strigis* (Gené) W. Dub." and "*Gabucinia* sp." Dubinin (1956: 224–226) treats two species which are distinguished on the base of data from the literature. In his own words:

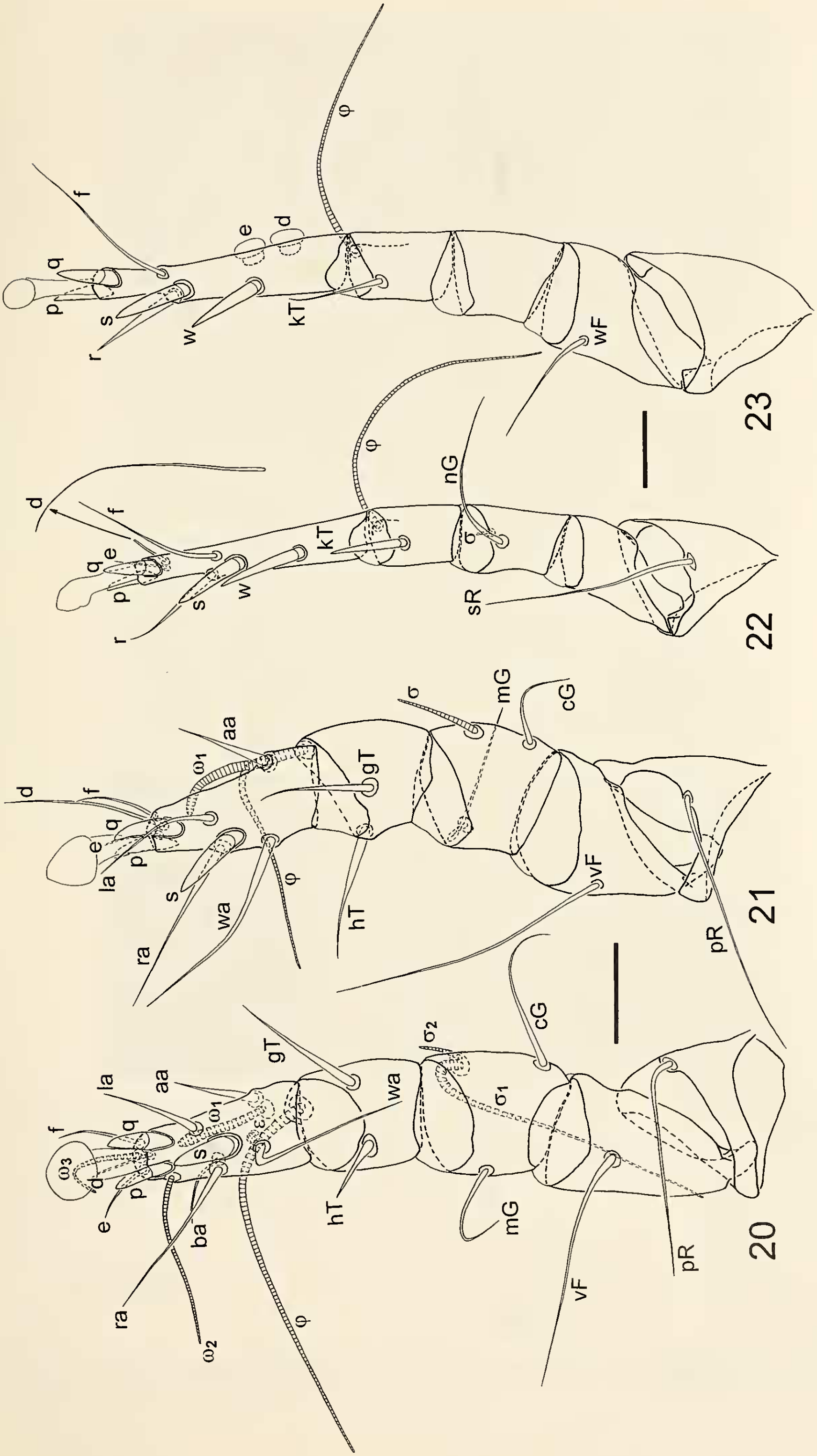
Figs. 17–19. *Tytodectes strigis*, male; optical sections (light micrographs) of different focal planes taken through retracted aedeagus. – 17. Superficial level; *T* = tip of aedeagus; – 18. middle level; *GP* = genital papillae; – 19. deepest level. – Scale bars: 20 µm.

1. *Gabucinia strigis* "... from the subcutaneous cellular tissue of the short-eared owl (*Asio flammeus* Pontopp.) and the long-eared owl (*Asio otus* L.), which were first described by Gené (1845, 1848) and later by Oudemans (1937) ... The deutonymphs of *Gabucinia strigis* (Gené) parasitize in the subcutaneous cellular tissue of the short- and long-eared owl of the genus *Asio* Schaeffer. The parasites can be found very frequently in fatty deposits at the surface of the breast muscles of the birds. The active developmental stages parasitizing on the vanes of the remiges are unknown. In the USSR, mites were found on the short-eared owl *Asio flammeus flammeus* (Pontopp.) in the Volga delta (nature reserve Astrakhan)." It is stated in a footnote: "I found the males and the females of this unknown species of the genus *Gabucinia* on the short-eared owl *Asio flammeus* (Pontopp.) in the Volga delta (the material is not preserved)." "Out of the territory of the USSR deutonymphs of *Gabucinia strigis* (Gené) were recorded in the short-eared owl *Asio flammeus flammeus* (Pontopp.) (= *Strix accipitrinus* Pall., *Otus accipitrinus*, *Strix flammea*) from Germany, Italy, France and Holland and in the long-eared owl *Asio otus otus* L. (*Stryx otus*, *Otus otus*, *Strix dominata* Pall.) from Italy."

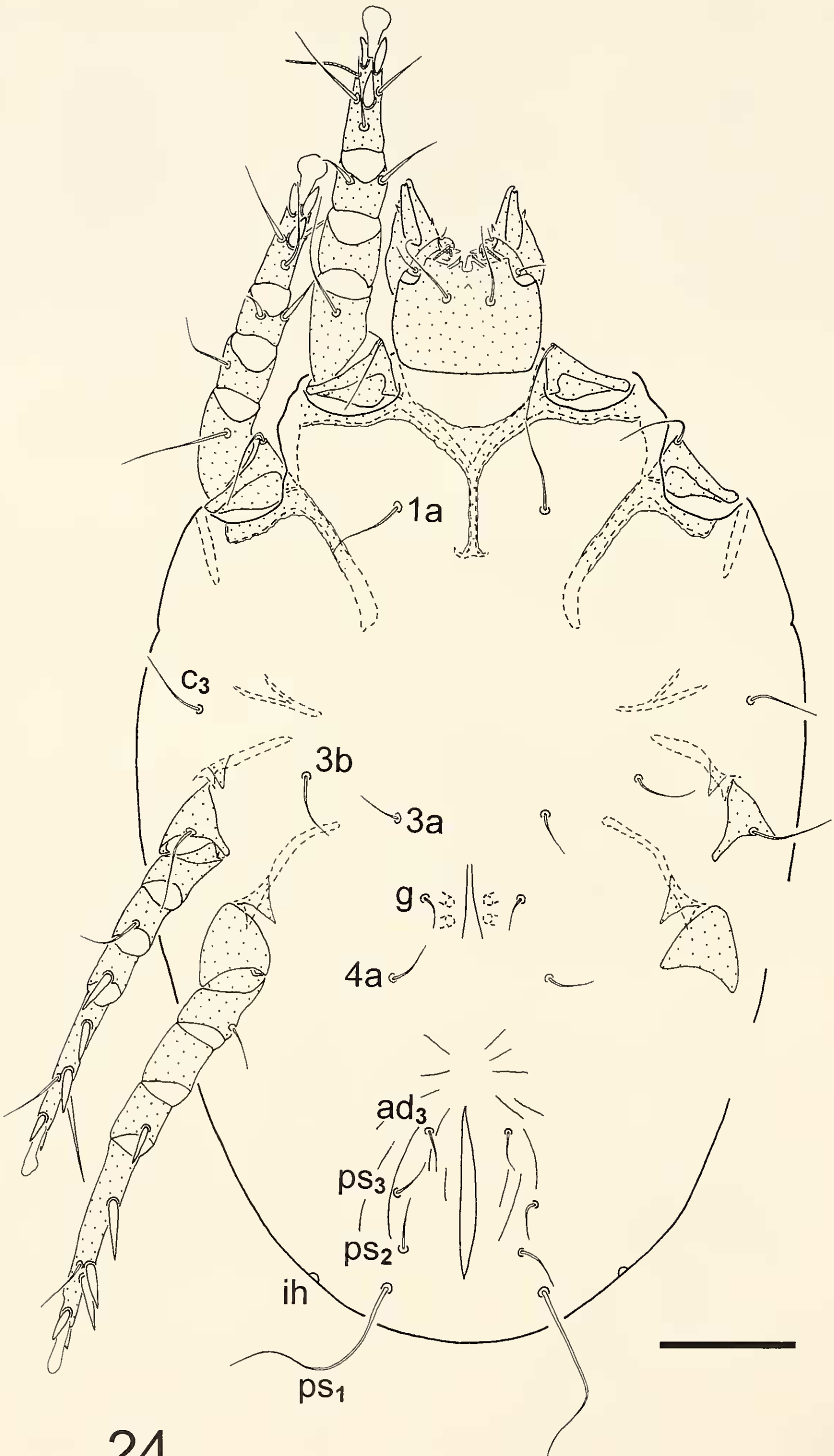
2. *Gabucinia* sp. "from the subcutaneous cellular tissue of barn owls (*Tyto alba* Scopoli), which are mentioned by Vitzthum [1933 (meaning 1934)] under the name '*Sarcoptes strigis*' ... They are undescribed and just incidentally mentioned in Vitzthum's article under the collective term '*Sarcoptes strigis*'."

In the investigation of subcutaneous deutonymphs of birds a decisive turn occurred when Fain & Bafort (1966, 1967) published the life cycle of *Hypodectes propus*. So far its deutonymphs had been assigned to the feather mite *Falculifer rostratus*. By investigating numerous pigeons nests, however, it was clearly shown that they are in fact members of a separate mite group, the deutonymphs of which go through a parasitic phase in the bird, whereas the other instars live in the nest material of these birds during their breeding period.

In the same year, Fain (1966) published a preliminary note, in which he erects a new genus "*Tytodectes*". As type species he selects *Tytodectes tyto*, a species newly described in the same paper and found in the African *Tyto alba affinis* (Zaire). In his comprehensive work on avain Hypoderatids Fain (1967a) gives additional characteristics for the genus *Tytodectes*. In respect to the host of "*Sarcoptes strigis*" he translates "barbagianni" into *Tyto alba* (p. 5). Based on the drawings of Oudemans (1937), Fain (1967a) places "*Sarcoptes strigis*" in the new genus *Tytodectes* and discusses the character differences in respect to *Tytodectes tyto*. Despite the inspection of about



Figs. 20–23. *Tytodectes strigis*, male. – 20. Leg I; – 21. leg II (scale bar figs. 20–21: 20 µm); – 22. leg III; – 23. leg IV (scale bar figs. 22–23: 20 µm).



24

Fig. 25. *Tytodectes strigis*; tritonymph ready for hatching, enclosed in protonymphal exuvia (light micrograph); *arrow*, inset: genital papillae of protonymph and tritonymph (scale bar: 30 µm); – inset: *arrows*: genital papillae of protonymph, *arrowhead*: genital papillae of tritonymph.

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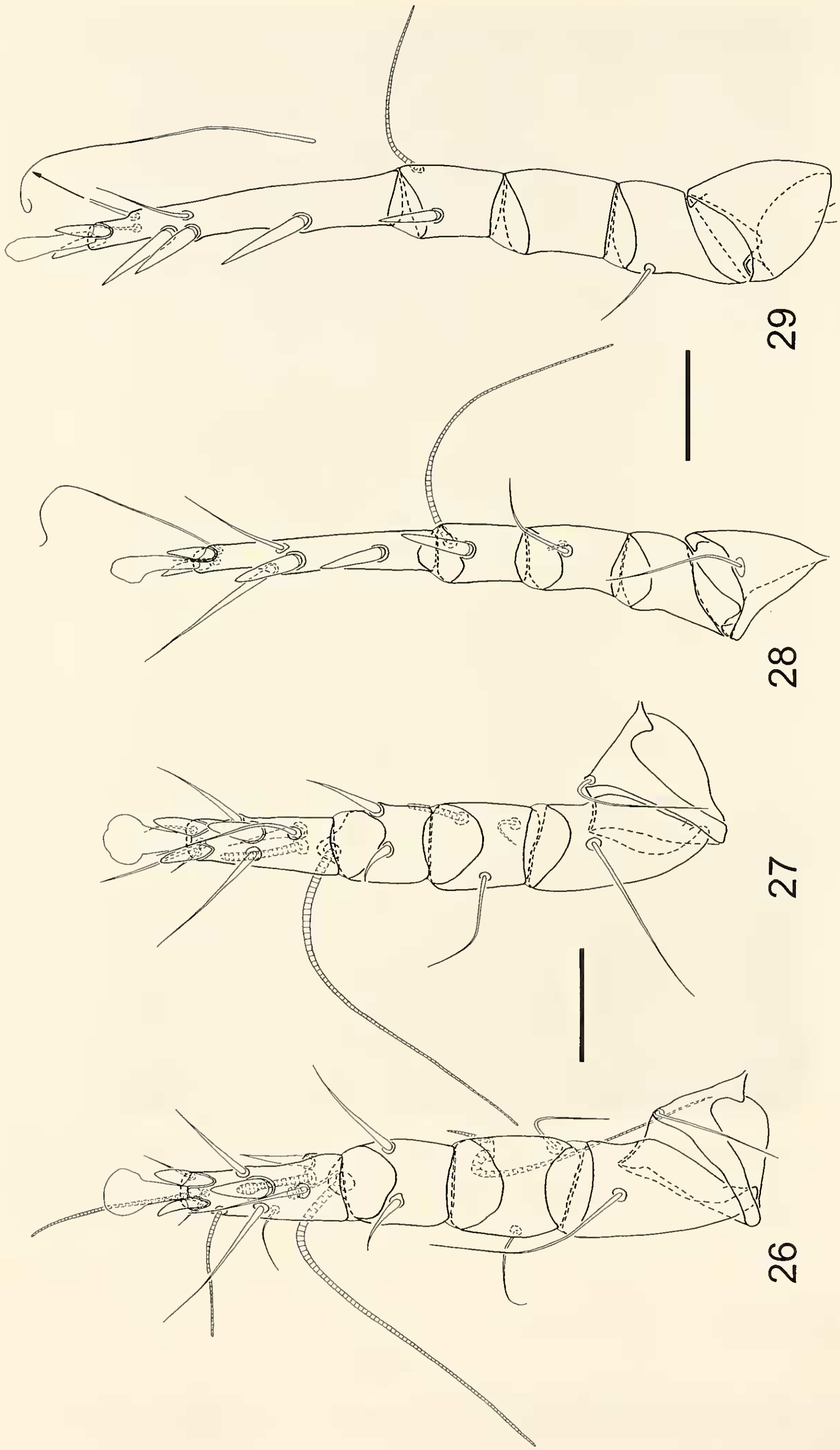
Fig. 24. *Tytodectes strigis*, tritonymph (directly developed from protonymph); ventral view, left legs partly omitted. – Scale bar: 40 µm.



Figs. 26–29. *Tytodectes strigis*, tritonymph. – 26. Leg I; – 27. leg II (scale bar figs. 26–27: 20 µm); – 28. leg III; – 29. leg IV (scale bar figs. 28–29: 20 µm).

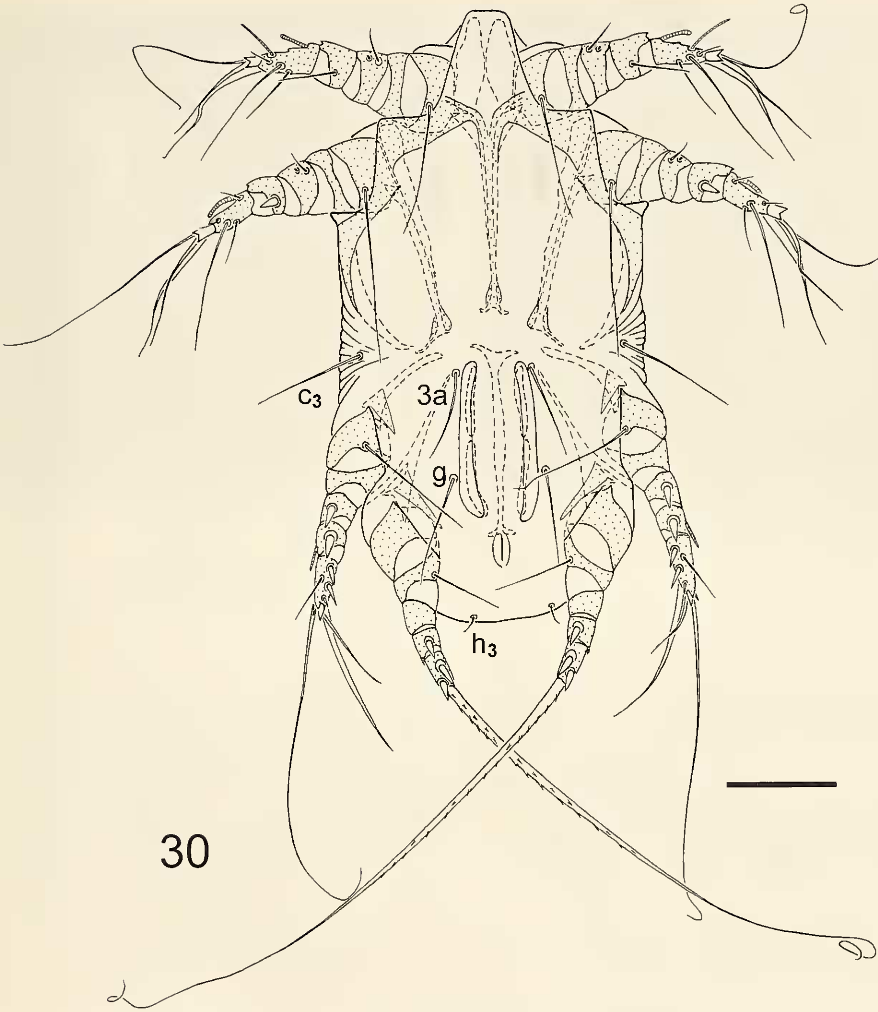


Fig. 30. *Tytodectes strigis*, young deutonymph; ventral view. – Scale bar: 40 µm.

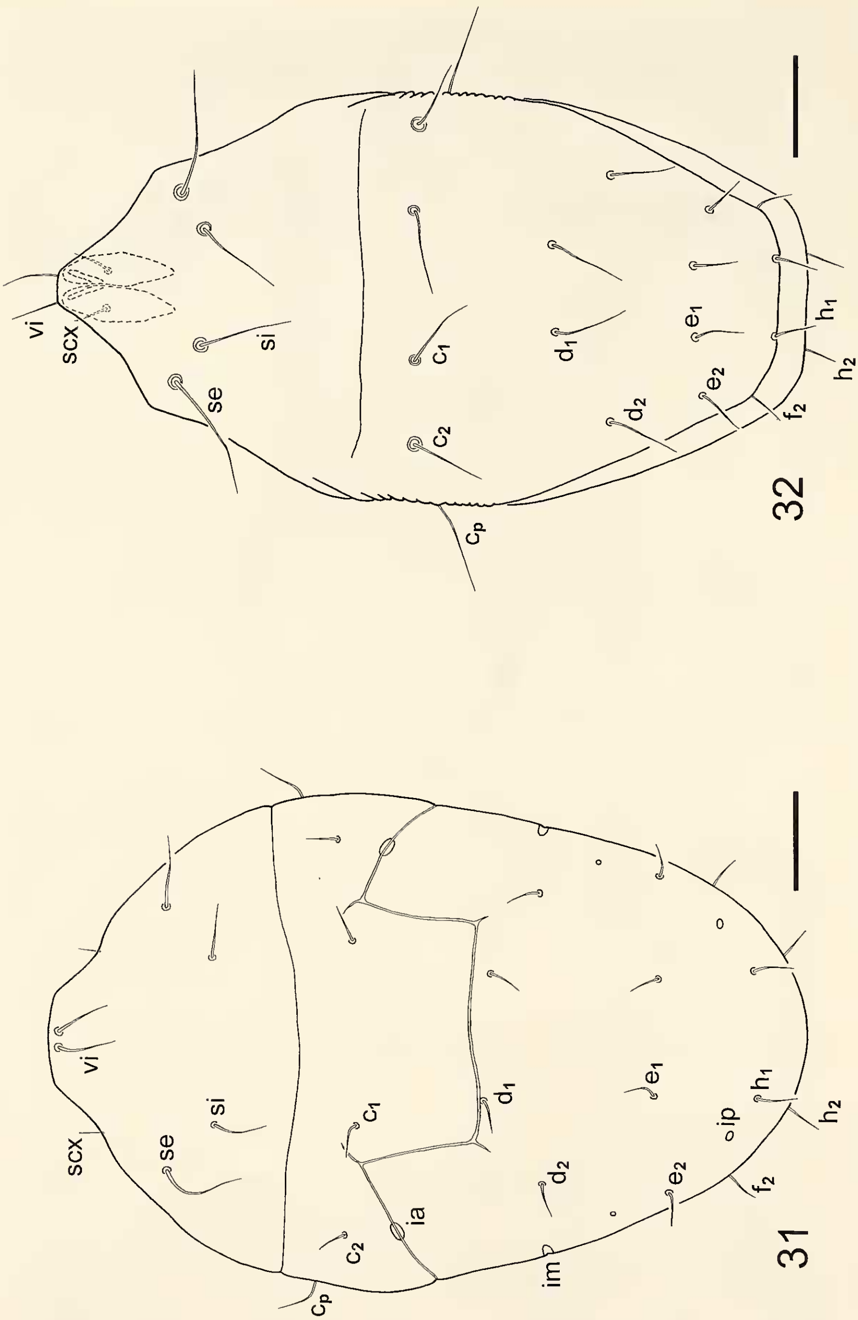
ten barn owls from different regions of Belgium, FAIN (1967a) did not succeed in recovering the hypopi of that species.

CERNY (1969) describes *Tytodectes glaucidii* from Cuba, which has been found in the breast and the hind leg of *Glaucidium siju siju*.

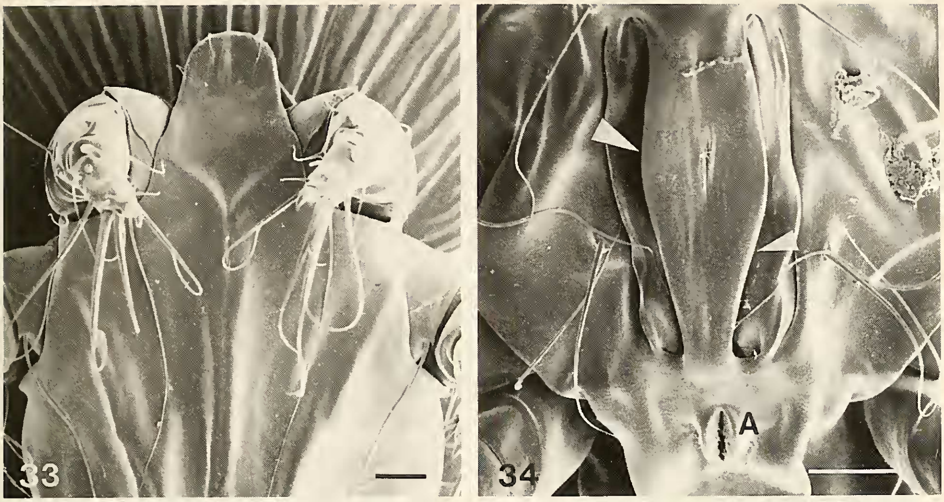
So far all the species of *Tytodectes* were only known as deutonymphs. In 1981, OCONNOR describes a female Hypoderatid from the nest of a pigmy owl (*Glaucidium* sp.) in Mexico. Since OCONNOR was not certain whether or not he had indeed found an adult representative of the genus *Tytodectes,* he prefers to introduce the new generic name "*Neotytodectes*" (*Neotytodectes mexicanus*) for that mite.

DOMROW (1992) reports *Tytodectes tyto* also from Tasmania (in *Tyto novaehollandiae*).

Finally we draw attention to the remarkable correspondence of several authors in respect to the location of the hypopi in the owl:



Figs. 31–32. *Tytodectes strigis*. – 31. Tritonymph (directly developed from protonymph); idiosoma, dorsal view (scale bar: 40 μm). – 32. young deutonymph; idiosoma, dorsal view (scale bar: 30 μm).



Figs. 33–34. *Tytodectes strigis*, young deutonymph. – 33. Proterosoma, ventral view; – 34. metapodosoma, ventral view; *arrowheads*: longitudinal slits leading to the genital papillae; *A* = anus. – Scale bars: 10 µm.

Creplin (1844): ". . . at the heel joint . . . of the foot, between the extensor tendon and the tibia" and "at the heel joint of both feet, . . . above of it, in the cellular tissue between the completely uninjured skin and the extensor tendon . . ."

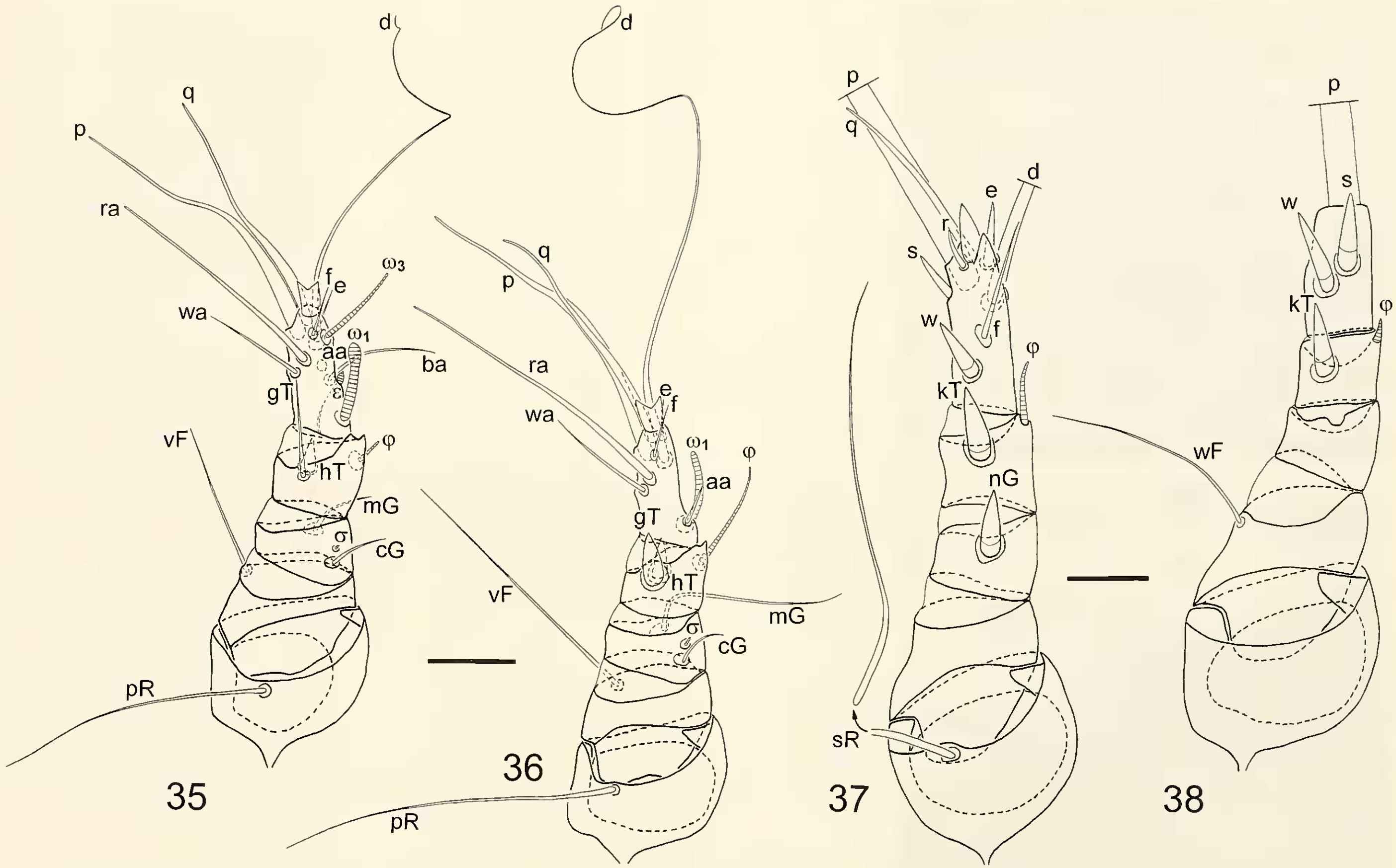
Gené (1848): "And the site, where these parasites are always and numerously found, is the cellular tissue and the fatty layer, which are situated between the skin and the muscles. Moreover one notices that the affected sites are constantly the legs, the thighs and the flanks, I never happened to find them at the front face of the chest, at the back, the wings or along the neck."

Domrow (1992): "Very numerous in subcutaneous tissues around hock joint."

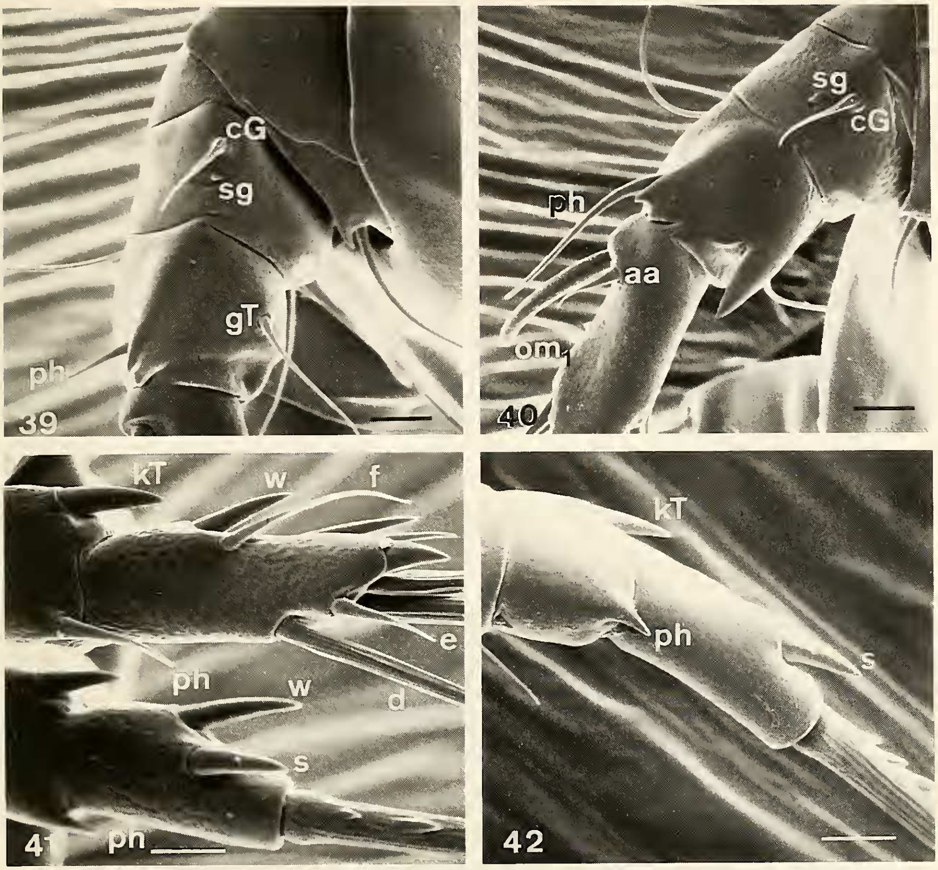
4. Identification of the Host Bird

As already mentioned in chapter 3, the term "*Strix flammea*" can be referred to *Tyto alba* as well as to *Asio flammeus*. Gené additionally uses "barbagianni" and the vernacular name "dama". "Barbagianni" still is the current name for the barn owl. Neither is there an entry in the dialect atlas of Jaberg & Jud (1930: map 508) for another local meaning of the name "barbagianni". Moreover, for seven localities in the vicinity of Torino "dama" is reported to be as synonym of the barn owl. Outside of Piedmont, "dama" does not appear at all in connection with owls. Considering this, Oudemans' (1937) equation of "barbagianni" with *Asio flammeus* and *A. otus* does not seem to be justified and seems to be the result of pure arbitrariness.

Finally, the interpretation of the existing literature by Dubinin (1956) is pure imagination. For example he fails to notice that Vitzthum (1934) and Oudemans (1937) refer to identical publications and that the two authors only interpret "*Strix flammea*" differently. He also takes mere citations of some authors as true records (e. g. Oudemans, 1937 does **not** mention an own finding in the Netherlands). The putative



Figs. 35–38. *Tytodectes strigis*, deutonymph. – 35. Leg I; – 36. leg II (scale bar figs. 35–36: 15 µm); – 37. leg III; – 38. leg IV (scale bar figs. 37–38: 10 µm).



Figs. 39–42. *Tytodectes strigis*, deutonymph. – 39. Leg I showing solenidion sigma (*sg*) on genu. Further *explications*: *cG*, *gT*: setae; *ph* = solenidion phi. – 40. Leg II showing solenidion sigma (*sg*) on genu. Further *explications*: *aa*, *cG*: setae; om_1 = solenidion omega 1; *ph* = solenidion phi. – 41. Leg III (above) and IV (below) showing solenidia phi (*ph*) on tibia III and IV. Further *explications*: *d*, *e*, *f*, *kT*, *s*, *w*: setae. – 42. Leg IV showing solenidion phi (*ph*) on tibia IV. Further *explications*: *kT*, *s*: setae. – Scale bars: 5 µm.

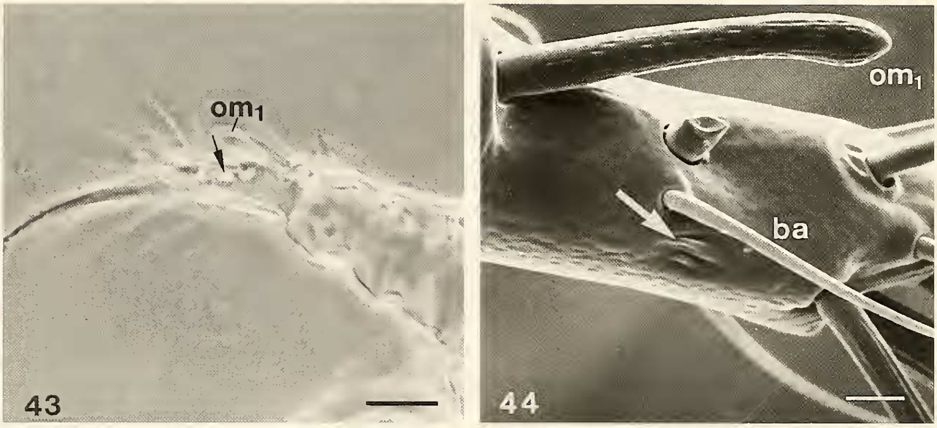
record of "*Gabucinia strigis*" from the short-eared owl doubtless applies to feather mites since he refers to "mites" and not to deutonymphs.

5. The Investigation of the Materials

Table 1 shows the results of the nestbox-surveys of barn owls, investigated in the years 1994–1996 and the findings of 1992. During the 1992 survey only the positive samples were registrated. Thus, they can not be used for statistical calculations.

All cases refer to first clutches.

Table 2 lists the results of the inspection of barn owls and gives the locations of the mites inside the bird.



Figs. 43–44. *Tytodectes strigis*, deutonymph. – 43. Leg I (light micrograph); *arrow*: notch in cuticle, resembling the socket of setae; om_1 = solenidion omega 1 (scale bar: 10 µm); – 44. leg I, tarsus; *arrow*: grooves in cuticle covering the notch of fig. 43; *ba*: seta; om_1 = solenidion omega 1 (scale bar: 2 µm).

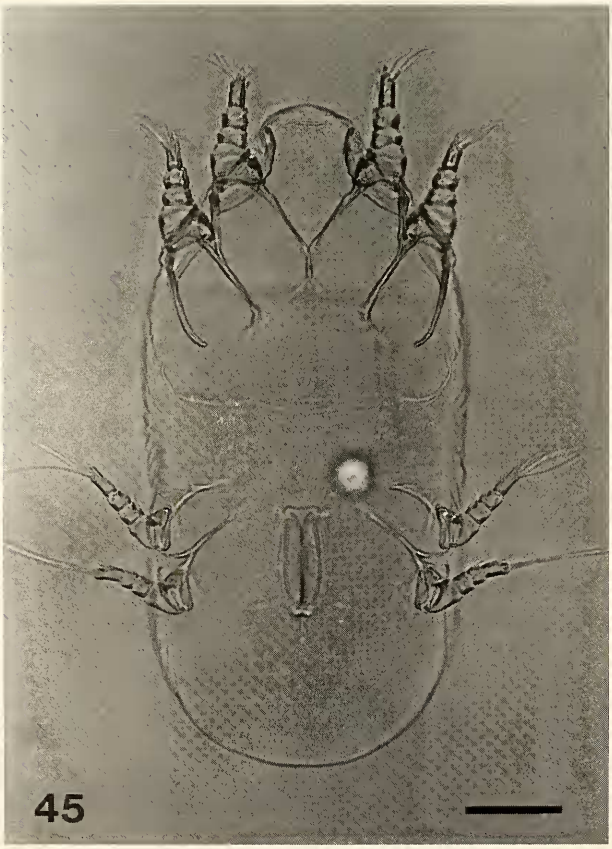


Fig. 45. *Tytodectes strigis*, enlarged deutonymph (light micrograph). – Scale bar: 60 µm.

6. Redescription of *Tytodectes strigis* (Gené, 1845)

Sarcoptes strigis Gené (1845) Atti della Riunione degli Scienziati italiani 6: 409–410 [vicinity of Torino].
Sarcoptes strigis Gené (1848): Studi Entomologici, 1: 371–376 table XVI.
Hypodectes strigis De Filippi (1861): Archivio per la Zoologia l'Anatomia e la Fisiologia 1 (1): 52–60.
Kramerella lunulata Oudemans (1937) [non Haller, 1878]: Kritisch Historisch Overzicht Der Acarologie, Vol. E: 2164–2168.
Gabucinia strigis Dubinin (1956): Fauna USSR. Arachnida 6, part 7. Feather Mites (Analgesoidea). Part 3. Pterolichidae: 224–226.
Gabucinia sp. Dubinin (1956): Fauna USSR. Arachnida 6, part 7. Feather Mites (Analgesoidea). Part 3. Pterolichidae: 226.
Tytodectes strigis Fain (1967): Bull. Inst. r. Sci. nat. Belg. 43 (4): 64.

Retroconjugate mites with facultative hypopody (figs. 25, 67). All instars in the nest of *Tyto alba*. Deutonymph parasitizing in the connective tissue of *Tyto alba*. All instars lack a demarcated propodosomatal shield. si shorter than se.

6.1. Adults

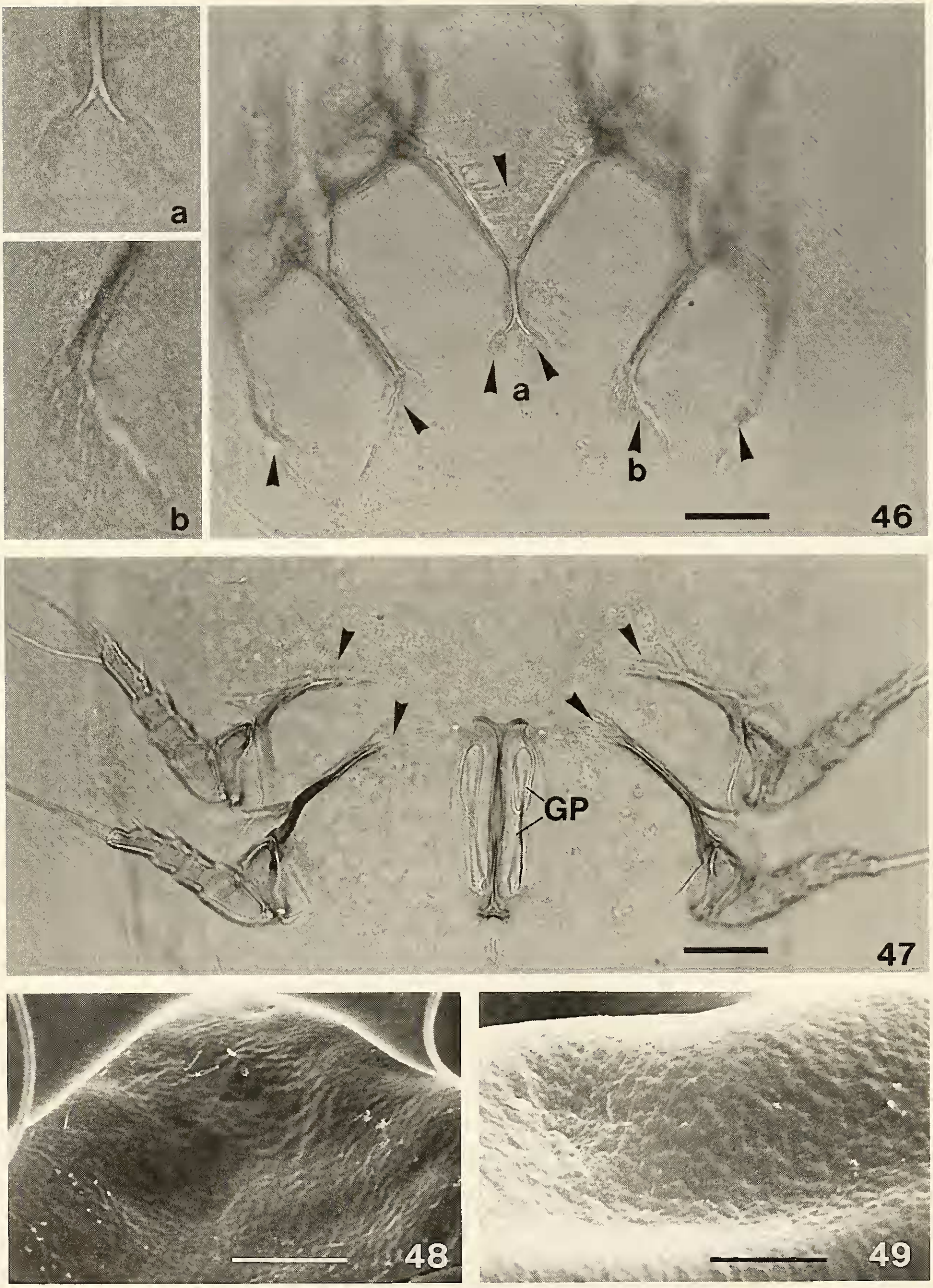
6.1.1. Male

Length of idiosoma about 320 µm, colour: beige; all setae smooth.

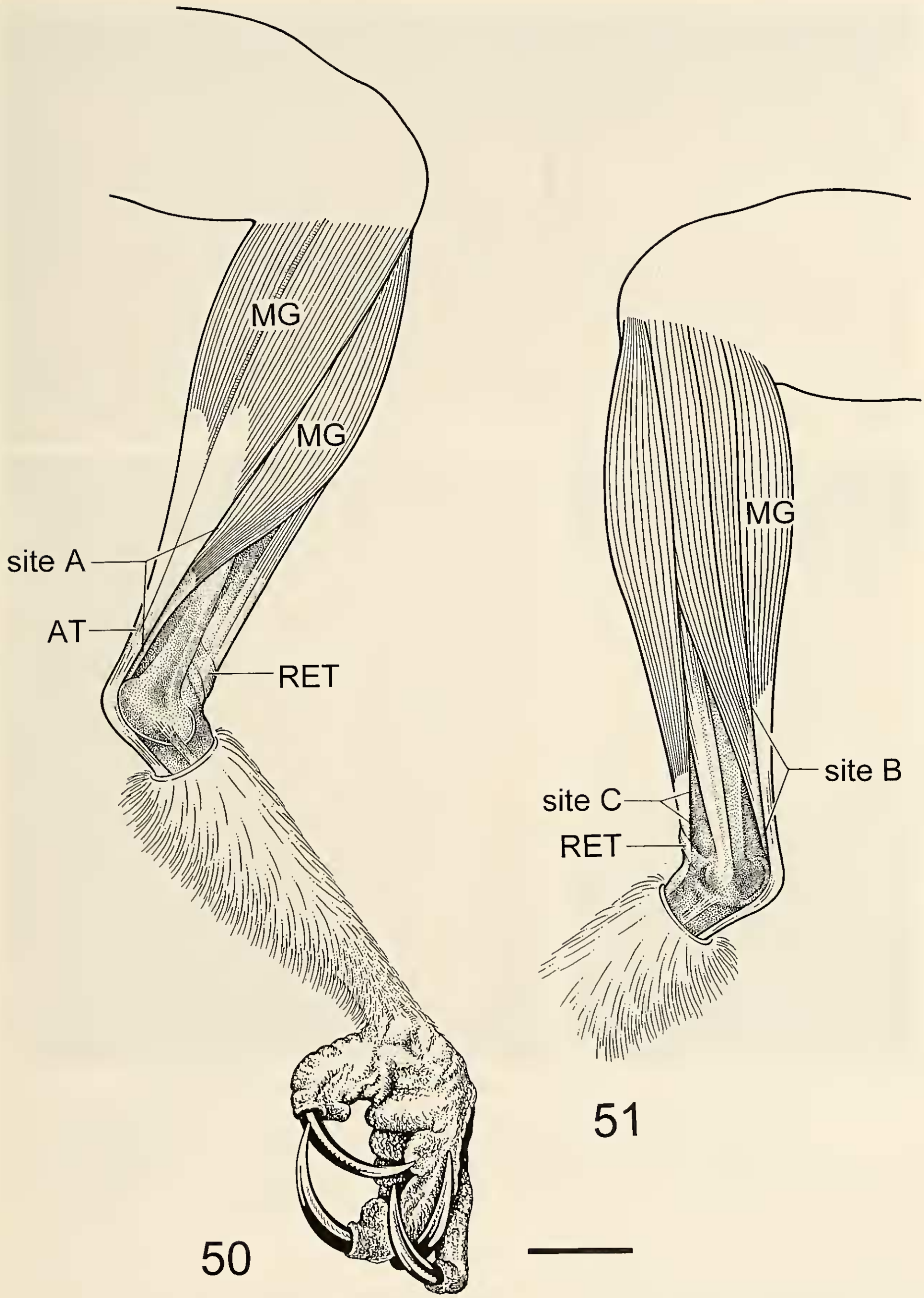
Dorsum (fig. 7): Idiosomal chaetome: scx, vi, si, se, c_1, c_2, c_p, d_1, d_2, e_1, e_2, f_2, h_1, h_2, ia, im, ip. – All hysterosomal setae short; the distances c_1–d_1, d_1–e_1, e_1–h_1 equal or larger than twice the length of the respective anterior seta. – A system of "oil grooves" covers the dorsal face of the hysterosoma; a transversal groove connects the "oil grooves" of both sides of the hysterosoma shortly in front of d_1; ia, im well developed and traversed in their longitudinal axis by an "oil groove". – End of opistho-

Table 3. Chaetotactic formulae for setae and solenidia of the legs of *Tytodectes strigis*.

	Setae			
	leg I	leg II	leg III	leg IV
larva	11.2.2.1.0	10.2.2.1.0	8.1.1.0.0	–
protonymph	11.2.2.1.0	10.2.2.1.0	8.1.1.0.0	5.0.0.0.0
deutonymph	9.2.2.1.1	8.2.2.1.1	8.1.1.0.1	3.1.0.1.0
tritonymph	11.2.2.1.1	10.2.2.1.1	8.1.1.0.1	8.1.0.1.0
adults	11.2.2.1.1	10.2.2.1.1	8.1.1.0.1	8.1.0.1.0
	Solenidia			
	leg I	leg II	leg III	leg IV
larva	1 + ε. 1.2.0.0	1.1.1.0.0	0.1.1.0.0	–
protonymph	2 + ε. 1.2.0.0	1.1.1.0.0	0.1.1.0.0	0.0.0.0.0
deutonymph	2 + ε. 1.1.0.0	1.1.1.0.0	0.1.0.0.0	0.1.0.0.0
tritonymph	3 + ε. 1.2.0.0	1.1.1.0.0	0.1.1.0.0	0.1.0.0.0
adults	3 + ε. 1.2.0.0	1.1.1.0.0	0.1.1.0.0	0.1.0.0.0



Figs. 46–49. *Tytodectes strigis*, deutonymph. – 46. Proterosoma of enlarged deutonymph exhibiting additional cuticular bundles at apodemes (*arrowheads*) formed during the stay in the host (light micrograph) (scale bar: 30 µm); insets *a*, *b*: details of indicated regions. – 47. Metapodosoma of enlarged deutonymph showing additional cuticular bundles (*arrowheads*) (light micrograph); *GP* = genital papillae (scale bar: 30 µm); – 48. dorsum of propodosoma (young deutonymph); fine structure of superficial cuticle (electron micrograph) (scale bar: 5 µm); – 49. same region as shown in fig. 48 but of enlarged deutonymph (electron micrograph) (scale bar: 5 µm).



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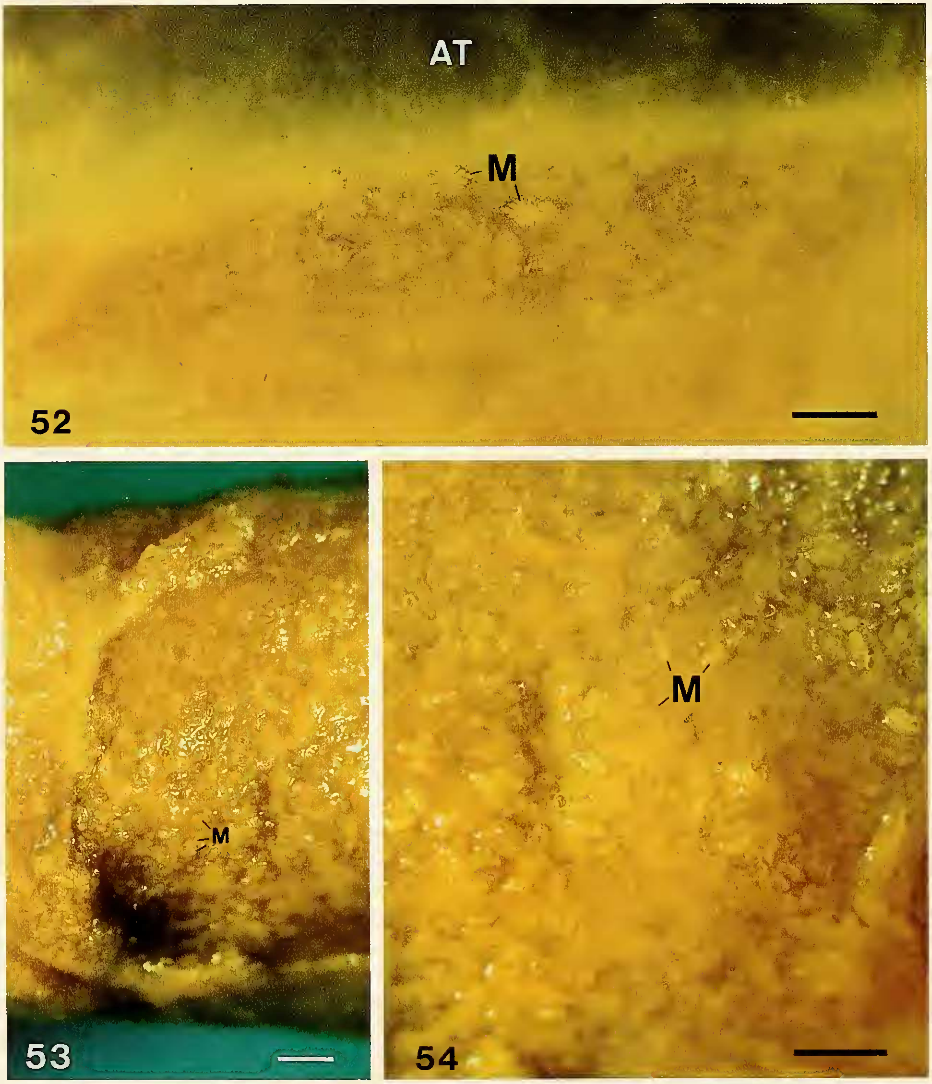
Figs. 50–51. *Tyto alba*; left leg (skin partly removed). – 50. Medial side showing one location of the mites (indicated as *site A*); *AT* = Achilles tendon. – 51. Lateral side showing the other locations of the mites (indicated as *site B* and *site C*). – Further *explications*: *MG* = musculus gastrocnemius, *RET* = retinaculum extensorium tibiotarsi. – Scale bar: 2.0 cm.



Figs. 52–54. *Tytodectes strigis*. – 52. Masses of swollen deutonymphs (*M*) in connective tissue along the achilles tendon (*AT*) (site A) (owl no. 1, right leg) (scale bar: 0.6 mm); – 53. heavy infestation in owl no. 13 (right leg); connective tissue densely interspersed with enlarged deutonymphs (*M*) (scale bar: 1.0 mm); – 54. detail of fig. 53 showing mites (*M*) surrounding fat bodies (scale bar: 0.9 mm).

soma concave; lateral parts of hysterosoma sclerotized, sclerotization originating dorsally posterior to an imagined line between e_2 and h_1.

V e n t r u m (fig. 12). Idiosomal chaetome: 1a, c_3, 3a, 3b, g, 4a, ps_1, ps_2, ps_3, ad_2, ih. – Epimerites I fused with epimera II, as well as epimerites II with epimera III; distal region of coxal fields I–IV sclerotized, sclerotization with branches along the apodemes of legs I and II. – Aedeagus (figs. 13–15, 17–19) strongly sclerotized, hidden

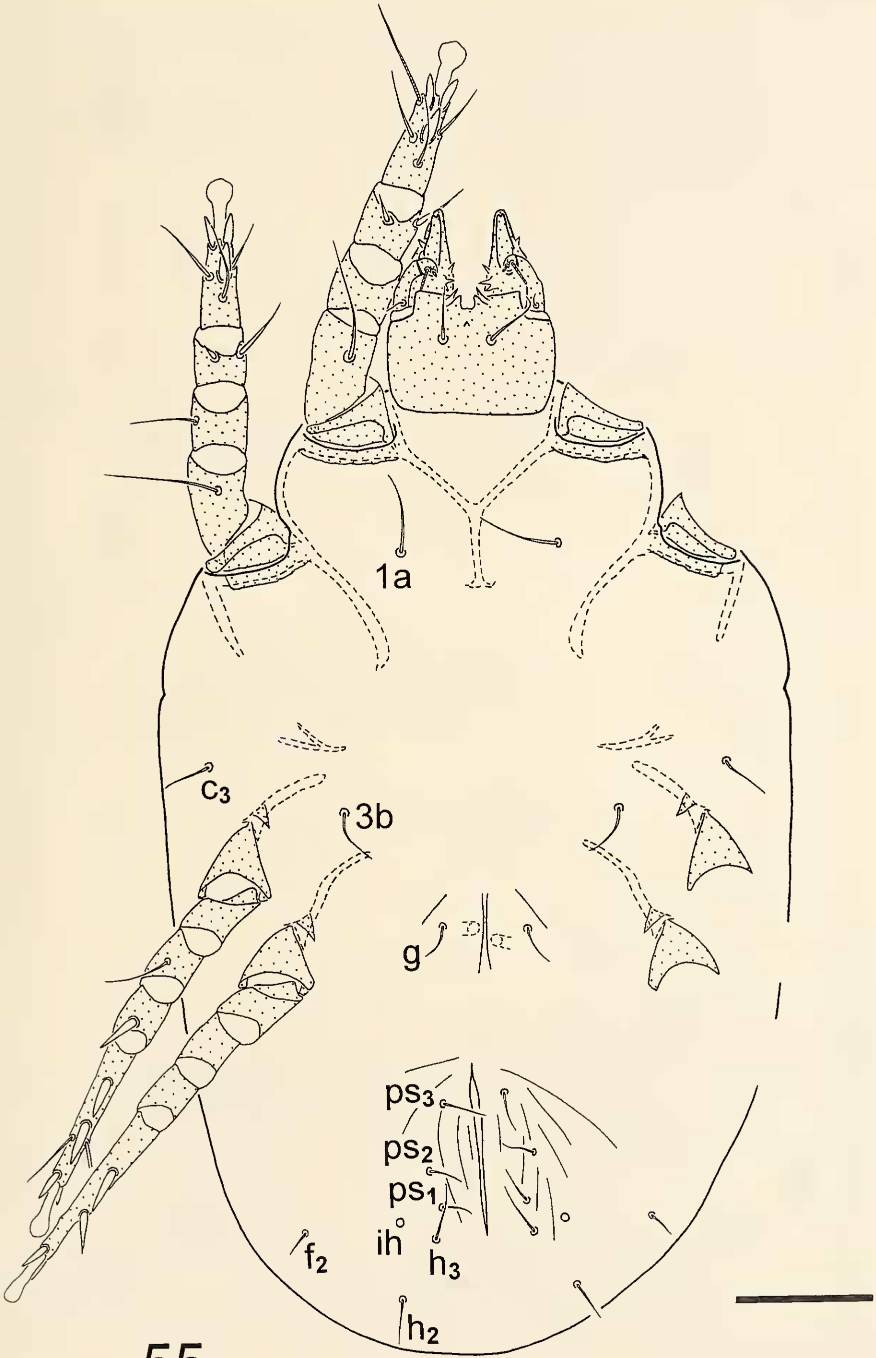


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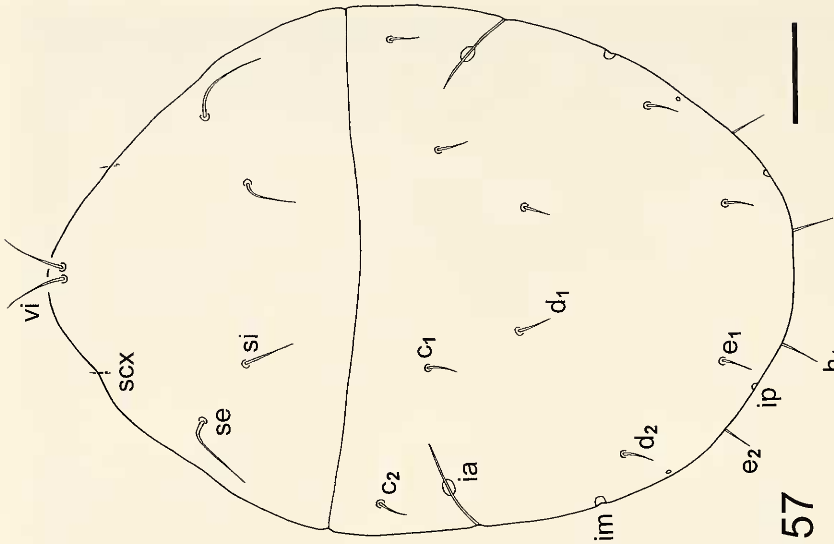
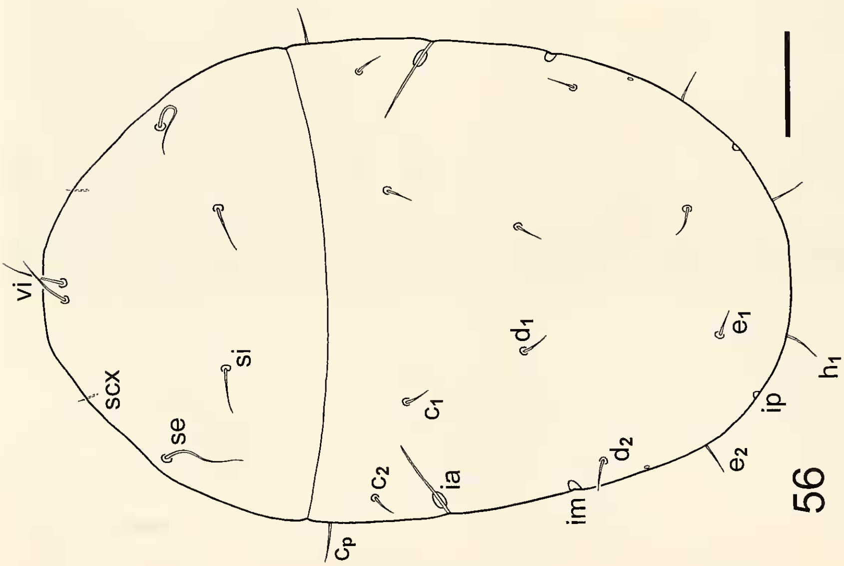
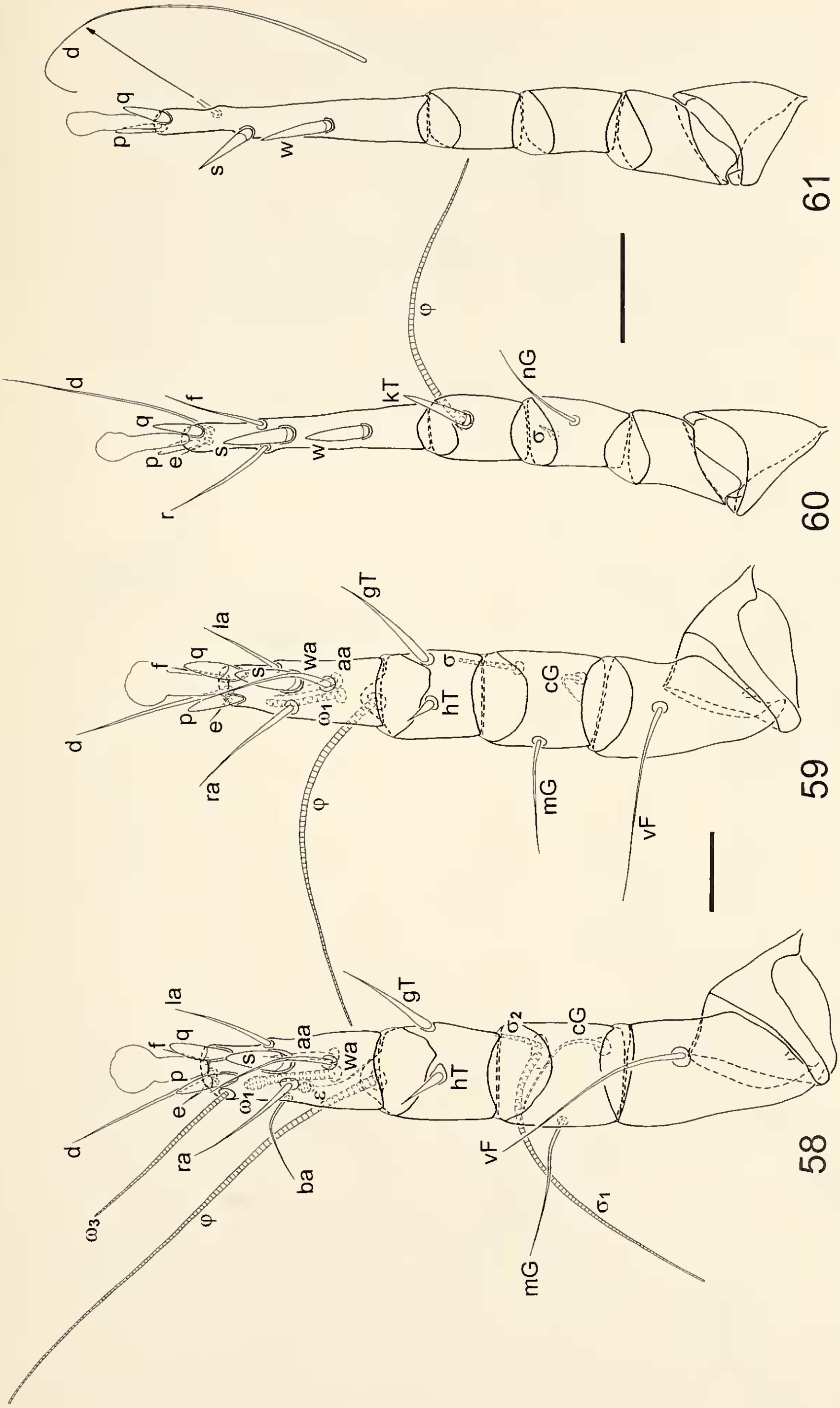
Fig. 55. *Tytodectes strigis*, protonymph; ventral view, left legs partly omitted. – Scale bar: 30 µm.





Figs. 56–57. *Tytodectes strigis*. – 56. Protonymph; idiosoma; dorsal view (scale bar: 30 µm); – 57. larva; idiosoma, dorsal view (scale bar: 25 µm).



Figs. 58–61. *Tytodectes strigis*, protonymph. – 58. Leg I; – 59. leg II (scale bar figs. 58–59: 10 µm); – 60. leg III; – 61. leg IV (scale bar figs. 60–61: 15 µm).

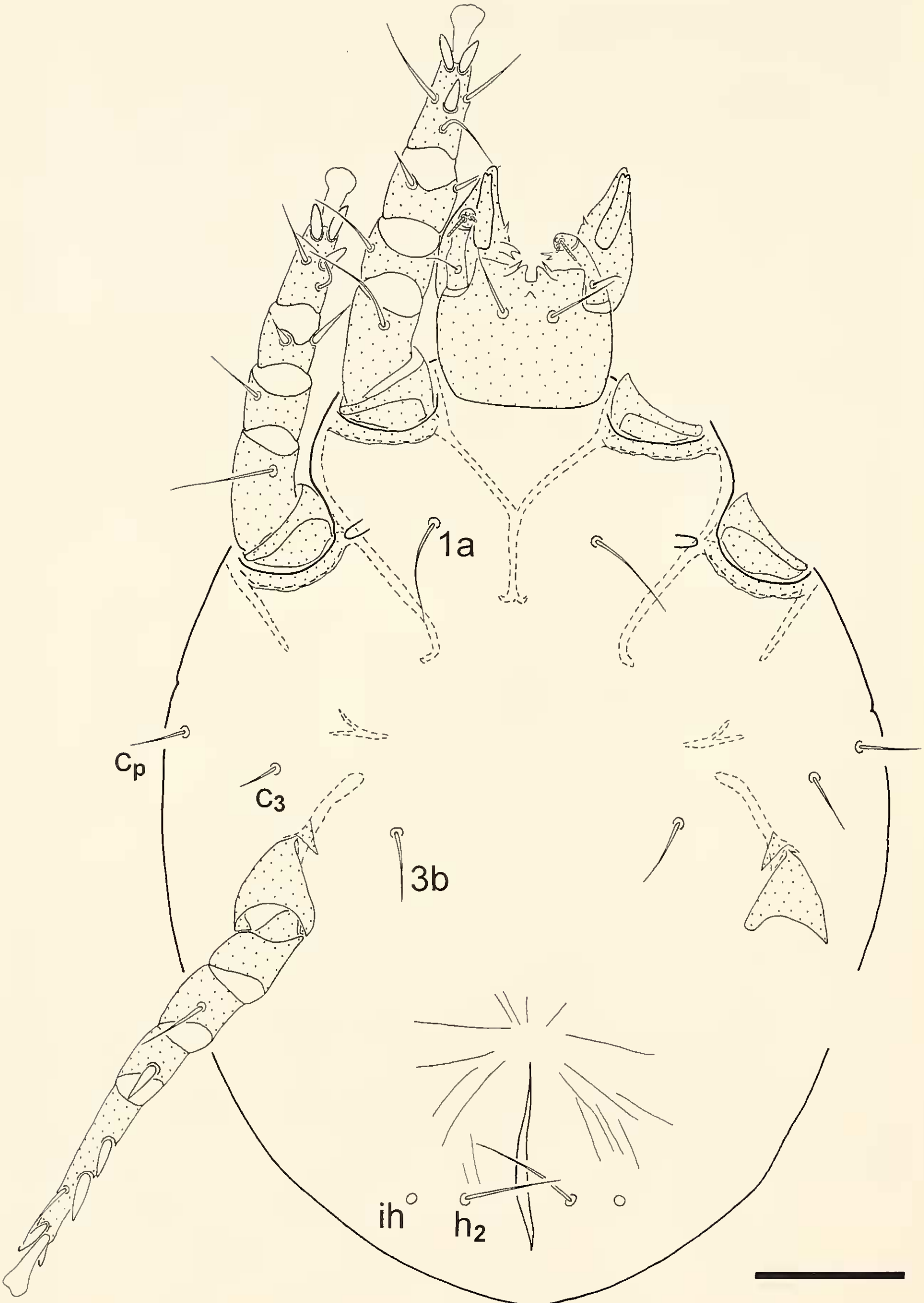


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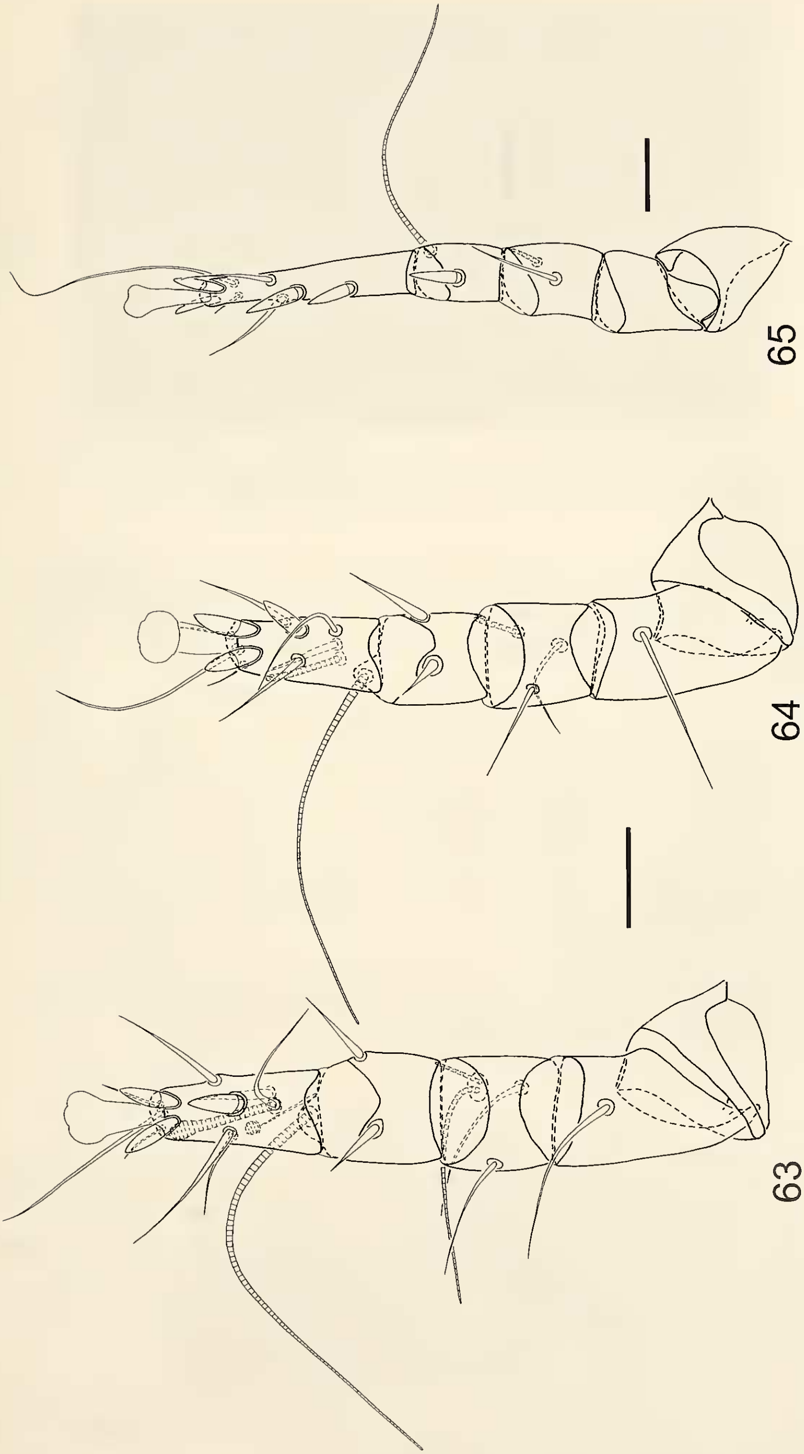
Fig. 62. *Tytodectes strigis*, larva; ventral view, left legs partly omitted. – Scale bar: 25 µm.



Figs. 63–65. *Tytodectes strigis*, larva. – 63. Leg I; – 64. leg II (scale bar figs. 63–64: 10 µm); – 65. leg III (scale bar: 10 µm).

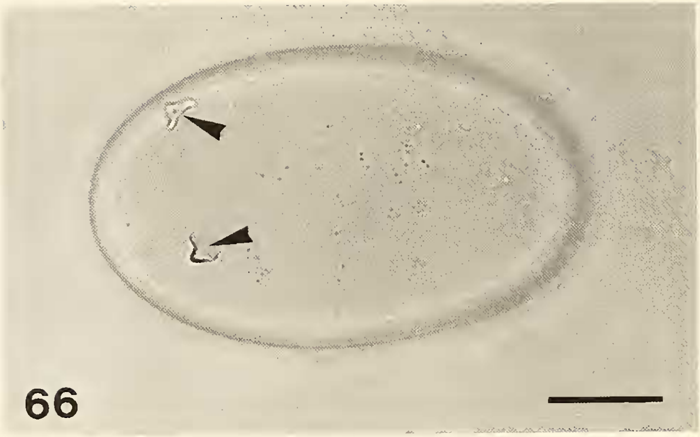


Fig. 66. *Tytodectes strigis*, egg (light micrograph); *arrowheads*: prelarval bosses which are supposed to be necessary for hatching. – Scale bar: 30 µm.

under genital folds forming a triangle; one pair of adanal copulatory suckers; the soft rim around the suckers covered with small bumps on its outer face (fig. 16).

Legs (figs. 20–23): Chaetome: see table 3.

6.1.2. Female

Length of idiosoma about 375 µm, colour: beige; all setae smooth.

Dorsum (figs. 2, 6): Idiosomal chaetome: scx, vi, si, se, c_1, c_2, c_p, d_1, d_2, e_1, e_2, f_2, h_1, h_2, h_3, ia, im, ip. – All hysterosomal setae except h_3 short; other length ratios and distances as described for male. – Between e_1 flat scale-like cuticular sculptering of variable size and number, sometimes missing. System of "oil grooves" as described for male. – Bursa copulatrix (figs. 3, 4) not very pronounced; for shape of basal parts of receptaculum seminis see fig. 5.

Ventrum (fig. 1): Idiosomal chaetome: 1a, c_3, 3a, 3b, g, 4a, ps_1, ps_2, ps_3, ad_3, ih. – Apodemes of legs and sclerotization of coxal fields as in the male. – Oviporus triangular with internal supporting structure.

Legs (figs. 8–11): Chaetome: see table 3.

6.2. Tritonymph

Tritonymph directly developed from protonymph: length of idiosoma about 315 µm, colour: beige; all setae smooth.

Dorsum (fig. 31): Idiosomal chaetome: as given for male. – All hysterosomal setae short; the distances c_1–d_1, d_1–e_1, e_1–h_1 larger than twice the length of the respective anterior seta. – System of "oil grooves" less well developed than in the adults; transversal groove shortly anterior to d_1; ia, im strongly developed, only ia traversed by an "oil groove".

Ventrum (fig. 24): Idiosomal chaetome: as given for female. – Epimerites I fused with epimera II; sclerotization of coxal fields similar to male, sclerotization along apodemes I and II, however, less well pronounced.

Legs (figs. 26–29): Chaetome: see table 3.

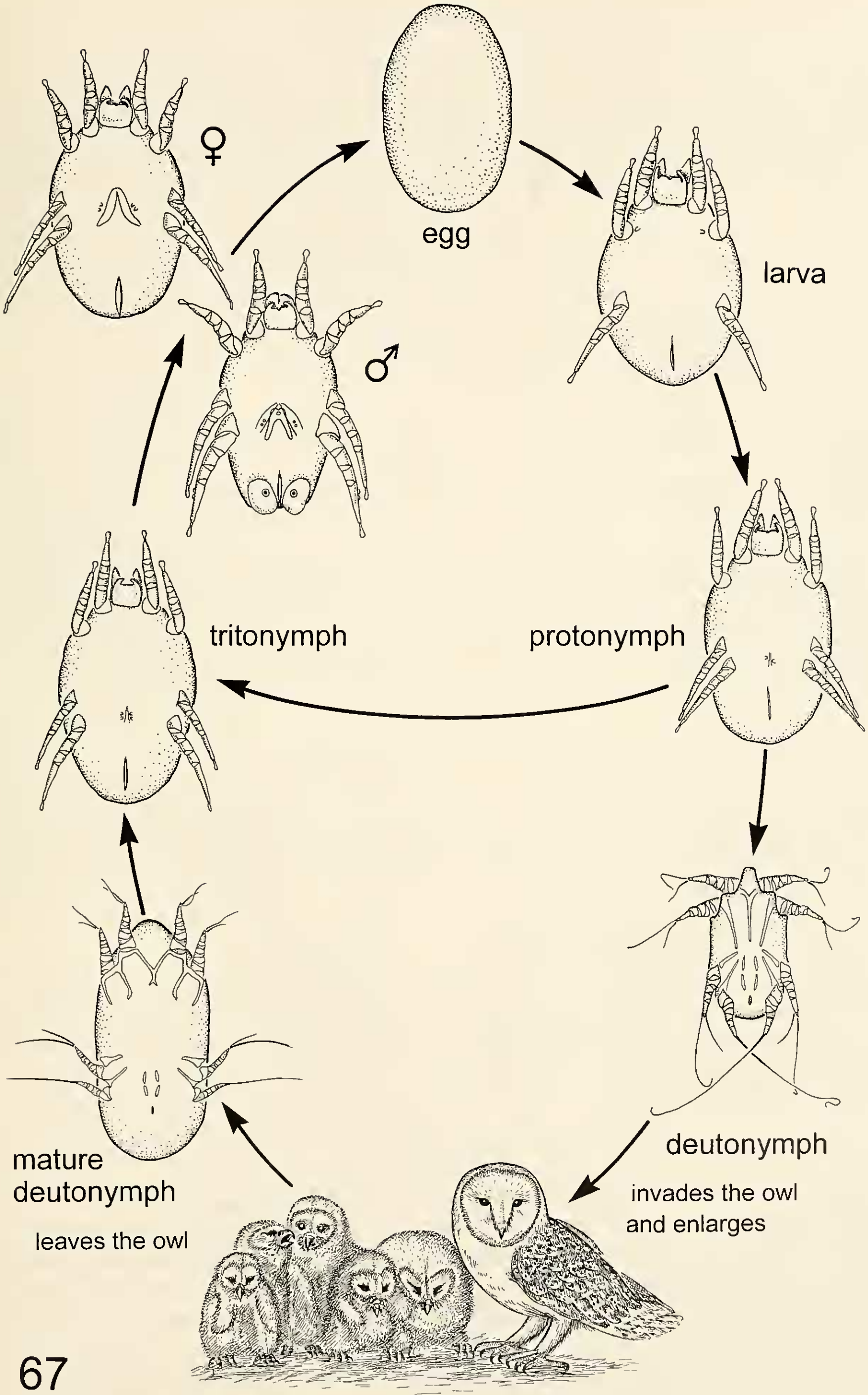


Fig. 67. *Tytodectes strigis*; schematic presentation of the life cycle.

6.3. Deutonymph

6.3.1. Description

6.3.1.1. Young deutonymph: Length of idiosoma about 215 µm, colour: white.

Dorsum (fig. 32). Idiosomal chaetome: scx, vi, si, se, c_1, c_2, c_p, d_1, d_2, e_1, e_2, f_2, h_1, h_2. – All hysterosomal setae short; c_1, c_2, and d_1, d_2 do not reach to the following row of setae.

Ventrum (figs. 30, 33, 34): Idiosomal chaetome: c_3, 3a, g, h_3. – Epimerites I fused with epimera II; cuticle sclerotized in the distal region of coxal fields I–IV as well as along the apodemes of leg I and II. Genital papillae on each side hidden in a pouch, which opens via a longitudinal slit to the outside (fig. 34).

Legs (figs. 35–44): Chaetome: see table 3.

6.3.1.2. Enlarged deutonymph (fig. 45): Length of idiosoma about 420 µm, colour: white.

Legs and chaetomes unchanged. Modifications originate mainly from stretching: region between legs I broadened; epimera I as well as epimerite I and epimeron II disjoined distally; the distance between the apodemes of legs I and II proximally increased, as well as the distance between the apodemes of legs III and IV. Structural alterations of exoskeleton: the apodemes and the region between epimera I are strengthened by additional deposition of cuticular material (figs. 46, 47) and the surface of the entire cuticle is rougher than in the young deutonymph (figs. 48, 49).

6.3.2. Taxonomic Remarks

1. In table 3 the total number of setae of tarsus I is given as 9, which is the normal number of setae of this leg segment in hypopi. This statement is based on the interpretation that seta aa is transformed into a strain detector: near ba (fig. 35) a circular thinning of the exoskeleton is situated, very similar to the socket of mechanosensitive bristles (fig. 43 *arrow*). This recess is covered by cuticle exhibiting several more or less parallel grooves (fig. 44 *arrow*).

2. Contrary to the description of the genus *Tytodectes* by Fain (1967a: 59) genus I and II bear one solenidion each (figs. 39, 40). We suppose, that these solenidia are also present in other species of *Tytodectes*, but have been overlooked until now because of their minuteness.

6.4. Protonymph

Length of idiosoma about 205 µm, colour: white; all setae smooth.

Dorsum (fig. 56): Idiosomal chaetome: scx, vi, si, se, c_1, c_2, c_p, d_1, d_2, e_1, e_2, h_1, ia, im, ip. – All hysterosomal setae short; all distances between the hysterosomal setae larger than twice the length of the respective anterior seta. – At each side an unbranched "oil groove"; ia, im strongly developed, only ia traversed by the "oil groove".

Ventrum (fig. 55): Idiosomal chaetome: 1a, c_3, 3b, g, f_2, h_2, h_3, ps_1, ps_2, ps_3, ih. – Epimerites I fused with epimera II; sclerotization of coxal fields similar to the male, sclerotization along the apodemes I and II lacking.

Legs (figs. 58–61): Chaetome: see table 3.

6.5. Larva and Egg

Length of idiosoma about 180 µm, colour; white; all setae smooth.

Dorsum (fig. 57): Idiosomal chaetome: scx, vi, si, se, c_1, c_2, d_1, d_2, e_1, e_2, h_1, ia, im, ip. – Otherwise as given for protonymph.

Ventrum (fig. 62): Idiosomal chaetome: 1a, c_3, cp, 3b, h_2, ih. – A pair of Claparède organs at coxal fields I; otherwise as given for protonymph.

Legs (figs. 63–65): Chaetome: see table 3.

Egg: (fig. 66) Length about 135 µm.

7. Observations on the Mites in the Nest Material

The mites could be reared in the laboratory in their natural substrate for about four months at moderate humidity. In order to clarify if the mites can also propagate under natural conditions without the presence of the owl, in 1996 nest material was collected from a few nestboxes already left by the fledglings (see table 1). One sample contained very few individuals of *T. strigis*. All instars, except the deutonymph, were present.

Except for the deutonymph all instars fed on the nest material. Since we were unable to observe tritonymphs having developed from mature deutonymphs, we cannot give any information whether these tritonymphs also feed on the nest substrate.

In most of the females, a longish structure projected from the bursa copulatrix, probably containing several spermatozoa (figs. 3, 4). These formations proved to be remarkably stable both in Hoyer's mountant and in the SEM-preparation. Even after their arrival in the receptaculum seminis they preserved their original shape at least for some time (fig. 3). Similar formations were described to occur in *Acarus* spp., *Lardoglyphus konoi*, *L. zacheri* and *Austroglycyphagus geniculatus* and interpreted as spermatophores (Griffiths & Boczek 1977, Boczek & Griffiths 1979).

8. Observations on the Mites in their Host

The deutonymphs were located exclusively in the subcutaneous tissue (Tela subcutanea) of the crus. Here, the mites were always concentrated at the medial side of the crus along and under the most superficial tendon of the musculus gastrocnemius (Achilles tendon) (site A) (figs. 50, 52). Additionally there were masses of hypopi at the analogous site of the lateral side of the crus (site B) (fig. 51) as well as under the tendons which pass under the retinaculum extensorium tibiotarsi (site C) (fig. 51). Moreover, in a few cases 1–4 isolated mites were scattered in the subcutis of the crus. The intensity of infestation ranged from a few individuals (owls nos. 10, 16, 19) up to hundreds of mites (owls nos. 12, 13, 15). In the latter cases the mites infiltrated the whole distal region of the crus (site D) from the sites A, B and C. A preferred orientation of the mites could not be registrated. Usually the mites were situated near small concentrations of adipose cells (fat bodies). Fig. 53 and 54 show a very high infestation, where the mites surround strongly corrugated fat bodies. Even in cases of massive infestation the surrounding tissue did not exhibit any indication of an immunological reaction at low magnifications. The enormous enlargement of the hypopi in the bird resulted mainly from the accumulation of fat. Whether this fat is directly derived from the host is yet unknown.

The cuticular alterations in the course of the swelling mainly affected the apodemes, which were strengthened by the adding of cuticular bundles (fig. 46, 47). These bundles radiate into the surrounding cuticle and effect the distribution of the forces onto larger regions of the exoskeleton. Additionally, the fine structure of the flat parts of the cuticule had been altered: on both light and electron microscopic images, the surface of the cuticle in the swollen deutonymphs appeared to be rougher than in the young hypopi (figs. 48, 49).

Because owl no. 19 died during its first attempts to fly, i. e. at age of 7–8 weeks, this allowed an estimate of the maximum time the deutonymphs need to attain their final size. The hypopi of this owl had already reached their maximal size. The light microscopic investigation (Hoyer's mountant) revealed that all the cuticular alterations described above were already completed after about eight weeks. This must not imply, however, that the mites had also achieved their physiological maturity for further development.

9. Discussion

Including the present description of the life history of *T. strigis* three developmental cycles of hypoderatid species are so far known (the other two being those of *Hypodectes propus* and *Suladectes hughesae antipodus*). Among them *T. strigis* adopts an extraordinary position because of the conservation of the facultative hypopody. All previously known life cycles of hypoderatid mites have one or several free living instars with reduced organs (mainly mouth parts and legs) indicating a reduction in the ability for direct development (*Suladectes hughesae antipodus*; Fain & Clark 1994) or necessitating it absolutely (*Hypodectes propus*; Fain & Bafort 1967).

The maintenance of the original developmental mode in *T. strigis* could be conditioned by the special reproductive biology of the barn owl, which may breed twice in years of high rodent populations. A continued propagation of the mites in the nest after it is left by the young owls is a prerequisite for the formation of deutonymphs which then can infest a possible second brood. If hypopi, having infested the parent birds during the first breeding, reach physiological maturity for further development only after the second brood has left the nest, the ability to reproduce independently of a host is the only possibility to use also the second brood for dispersal. If the mites are able to survive in the nest even until the beginning of the breeding in the subsequent year has to be clarified in further investigations. The ability for propagation in the absence of the owls and without the continuous provision with fresh substrate was clearly proved both by rearing experiments in the laboratory and by field observations.

A remarkable discrepancy exists between the prevalence of the mites in the barn owls (63 %) and the prevalence of mites in nest material (7 %). As an explanation three possible hypotheses can be put forward:

1) If the period of time in which the mature mites leave the parent birds is broadly distributed over the time of breeding and feeding, our collection of nest material could have been too early in some cases to find the mites.
2) In the case of a very low population density, the mites were not detected in some of the samples, especially if all the mites had died because of a probable deterioration of their living conditions.
3) There are additional ways of propagation and transmission beyond the breeding periods of the barn owl.

The comparison of the findings in owl no. 19 with the results of the sampling from the respective nest supports hypothesis 2. The small number of mites in this bird indicates a very low population density in the nest. Hypothesis 1 has to be tested in further investigations. To do this it is planned to collect nest material from several breeding places in regular intervals in order to determine in which phase of the breeding the first mites appear in the nest.

Compared with the extensive alterations of the exoskeleton (removal and complete reconstruction of apodemes) of the deutonymph of *Hypodectes propus* during its stay in the pigeon (FAIN 1967a), the cuticular changes in *T. strigis* in the course of its swelling in the host appear to be rather moderate. The changes result mainly from stretching caused by the strong increase in volume, whereby the apodemes are partly drawn apart. A prerequisite for this is a renewed plasticization of large regions of the cuticle. The renewed plasticization of parts of the cuticle after ecdysis has similarly been shown in a blood sucking insect (*Rhodnius prolixus*). Its control and mechanism has been investigated in manyfold approaches (overviews in NEVILLE 1975: 279–283 and REYNOLDS 1985). The addition of new cuticular material after hatching has also been observed in numerous insect species where it affects diverse regions of the exoskeleton (NEVILLE 1975: 235–253).

The poor immunological response the birds showed even in massive infestations with *T. strigis* is astonishing but seems to hold generally for the relation of hypoderatid deutonymphs and their hosts. Only ZÜRN (1882: 208) reports on calcifications of the wall of large blood vessels in animals infested by hypoderatid deutonymphs in that area. The infestation of two *Ibis* (*Tantalus*) *leucocephalus* by hypoderatid deutonymphs is described in detail by KUTZER & GRÜNBERG (1962). Likewise, no sign of inflammations were detected macroscopically. The connective tissue adjacent to the hypopi in histological inspection revealed only "weak signs (schwache Ansätze)" of an immunological reaction. From the fat bodies in the vicinity of the deutonymphs the lipids had been washed out. In which way the deutonymphs evade the immunological defence of their hosts is completely unknown. These and other important questions concerning the biology of the Hypoderatidae (e. g. mechanisms of invasion and emergence, the timing oft the latter, the mode of ingestion in the bird, modifications of the cuticle), however, can only be answered in laboratory experiments under controlled conditions.

10. References

BOCK, C. (1987): Einfache Schnellpräparationsmethode mit Carnoy und Hexamethyldisilazan für das REM. – Optik (Suppl. 3) **77**: 7; Stuttgart.

BOCZEK, J. & GRIFFITHS, D. A. (1979): Spermatophore production and mating behaviour in the stored product mites *Acarus siro* and *Lardoglyphus konoi*. – *In*: RODRIGUEZ, J. G. (ed.): Recent advances in Acarology. – Vol. **1**: 279–284; New York etc.

CERNY, V. (1969): The hypopi of Hypoderidae (Sarcoptiformes) parasitizing Cuban birds. – Folia Parasitologica **16**: 271–274; Praha.

CREPLIN, F. C. H. (1844): Endozoologische Beiträge. – Arch. Naturgesch. 10 (1): 112–133 + table 3; Berlin.

DE FILIPPI, F. (1861): *Hypodectes* – nuovo genere di Acaridi proprio degli uccelli. – Archivio per la Zoologia l'Anatomia e la Fisiologia **1** (1): 52–60 + table 5; Genova.

DOMROW, R. (1992): Acari Astigmata (excluding Feather Mites) parasitic on Australian vertebrates: an annotated checklist, keys and bibliography. – Invertebrate Taxonomy **6**: 1459–1606; East Melbourne, Victoria.

Dubinin, W. B. (1956): Fauna USSR. Arachnida 6, part. 7. Feather Mites (Analgesoidea). Part 3. Pterolichidae. – 814 pp.; Moscow. [in Russian]

Fain, A. (1966): Note sur les acariens nidicoles à deutonymphe parasite tissulaire des oiseaux (Hypodectidae: Sarcoptiformes) (Note préliminaire). – Revue Zool. Bot. afr. **74** (3–4): 324–330; Bruxelles.

– (1967a): Les hypopes parasites des tissus cellulaires des oiseaux (Hypodectidae: Sarcoptiformes). – Bull. Inst. r. Sci. nat. Belg. **43** (4): 1–139; Bruxelles.

– (1967b): Solenidiotaxy of leg I in the hypopy of the Acaridiae (Acari: Sarcoptiformes). – Revue Zool. Bot. afr. **76** (3–4): 244–248; Bruxelles.

Fain, A. & Bafort, J. (1966): Les hypopes parasitant les tissus cellulaires des pigeons sont les deutonymphes d'un acarien libre et pas celles d'un acarien plumicole (Note préliminaire). – Revue Zool. Bot. afr. **74** (3–4): 313–316; Bruxelles.

– (1967): Cycle évolutif et morphologie de *Hypodectes* (*Hypodectoides*) *propus* (Nitzsch) acarien nidicole à deutonymphe parasite tissulaire des pigeons. – Bull. Acad. r. Belg. (Cl. Sci., 5e Série) **53**: 501–533; Bruxelles.

Fain, A. & Clark, J. M. (1994): Description and life cycle of *Suladectes hughesae antipodus* subspec. nov. (Acari: Hypoderatidae) associated with *Sula bassana serrator* Gray (Aves: Pelecaniformes) in New Zealand. – Acarologia **35** (4): 361–371; Paris.

Gené, G. (1844, publ. 1845): Sopra un nuovo acaridio della *Strix flammea* (Adunanza del 23 settembre 1845). – Atti della Riunione degli Scienziati italiani **6**: 409–410; Torino.

– (1848): Brevi cenni su un Acaridio del genere de'Sarcopti che vive sulla *Strix flammea* (scritto postumo). – Studi Entomologici **1**: 371–376 + table 16; Torino.

Griffiths, D. A. (1964): A revision of the genus *Acarus* L., 1758 (Acaridae, Acarina). – Bull. Br. Mus. nat. Hist. (Zoology) **11**: 415–464; London.

Griffiths, D. A., Atyeo, W. T., Norton, R. A. & Lynch, C. A. (1990): The idiosomal chaetotaxy of astigmatid mites. – Journal Zoology **220**: 1–32; London.

Griffiths, D. A. & Boczek, J. (1977): Spermatophores of some acaroid mites (Astigmata: Acarina). – Int. J. Insect Morphol. & Embryol. **6** (5/6): 231–238; Oxford etc.

Grünberg, W. & Kutzer, E. (1962): Deutonymphen von Federmilben in der Subcutis von *Tantalus leucocephalus* (Indischer Nimmersatt). – Z. ParasitKde. **21**: 542–559: Berlin etc.

Hartert, E. (1912–21): Die Vögel der paläarktischen Fauna. – Vol. 2, 932 pp.; Berlin [Autorisierter Nachdruck 1969; Lehre].

Jaberg, K. & Jud, J. (1930): Sprach- und Sachatlas Italiens und der Südschweiz. – Vol. **3**; Zofingen.

Mégnin, P. (1879): Les acariens parasites du tissu cellulaire et des réservoirs aériens chez les oiseaux. – J. Anat. Physiol. **15**: 123–153 + tables 7–8; Paris.

Neville, A. C. (1975): Biology of the arthropod cuticle. I–XVI. – 448 pp.; Berlin etc.

OConnor, B. M. (1981): A new genus and species of Hypoderidae (Acari: Astigmata) from the nest of an owl (Aves: Strigiformes). – Acarologia **22** (3): 299–304; Paris.

Oudemans, A. C. (1937): Kritisch Historisch Overzicht Der Acarologie. – Vol. E., pp. 2164–2168; Leiden.

Peters, J. L. (1940): Check-list of birds of the world. – Vol. **4**, 291 pp.; Cambridge, Mass. [Reprinted 1964].

Raikow, R. J. (1985): Locomotor system. – *In*: King, A. S. & McLelland, J. (eds.): Form and function in birds. – Vol. **3**, pp. 57–147; London etc.

Reynolds, S. E. (1985): Hormonal control of cuticle mechanical properties. – *In*: Kerkut, G. A. & Gilbert, L. I. (eds.): Comprehensive insect physiology, biochemistry and pharmacology. – Vol. **8**, pp. 335–351; Oxford etc.

Robin, C. & Mégnin, P. (1877): Mémoire sur les sarcoptides plumicoles. – J. Anat. Physiol. **13**: 209–248 + tables 12–13; Paris.

Salomon, F.-V. (1993): Lehrbuch der Geflügelanatomie. – 479 pp.; Stuttgart.

Vitzthum, H. Graf (1934): Die endoparasitische Deutonymphe von *Pterolichus nisi*. – Z. ParasitKde. **6** (2): 151–169; Berlin.

Zürn, F. A. (1882): Die Krankheiten des Hausgeflügels. I–XVI. – 237 pp.; Weimar.

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